EFFECTS OF *JUNIPERUS VIRGINIANA* ENCROACHMENT ON PLANT AND AVIAN DIVERSITY IN OKLAHOMA CROSS TIMBERS FORESTS

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EFFECTS OF *JUNIPERUS VIRGINIANA*

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CROSS TIMBERS FORESTS

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CHAPTER I

INTRODUCTION

Eastern redcedar (*Juniperus virginiana* L. Cupressaceae) is a coniferous tree native to most of the United States east of the Rocky Mountains. Its abundance in the central United States, however, has increased dramatically over the past century due largely to anthropogenic fire suppression (Burkhardt and Tisdale 1976). The species was historically confined to rocky areas, mesic forests or places that otherwise rarely burned, but the species has now spread over many areas that used to be frequented by seasonal fires, such as grasslands and upland forests (Ormsbee et al. 1976, Lawson 1986).

As a species expanding into new habitats, redcedar has effects on the environment that differ from the species that once occupied regularly burned areas. The spread of redcedar in native grasslands and the consequences of this on the physical environment (grassland structure, soils, humidity) and on the biological environment (vegetation composition and richness) have been well studied (Lassoie et al. 1983, McBain 1983, Gehring and Bragg 1992, Norris et al. 2001, Bekele et al. 2006, Linneman and Palmer 2006, Knapp et al. 2008). The effects are not limited to vegetation, however, as redcedar also causes shifts in avian and mammalian species composition (Chapman et al. 2004, Coppedge et al. 2001, Horncastle 2004, Walker and Hoback 2007).

The encroachment of redcedar in forested areas is less apparent to the eye than incursions of this conifer into grasslands, especially in summer when the deciduous species that form a canopy over redcedar have leafed out. However, in spite of the absence of obvious changes in landscape appearance, encroachment of redcedar in wooded areas due to fire suppression causes important alterations in the functioning of forested ecosystems. In the Cross Timbers, a forested region at the edge of the prairie biome that extends from southern Kansas to central Texas, eastern redcedar forms dense midstories under a canopy dominated by post (*Quercus stellata*) and blackjack oaks (*Q.*

marilandica). These forests formerly only had a scattered midstory of deciduous shrubs and the occasional redcedar tree, interspersed with patches of prairie. Now they often have a dense midstory of a coniferous, evergreen species. The exact consequences of this redcedar midstory encroachment on the physical and biological environment have not been determined, but are likely important in terms of community composition and richness of understory vegetation and animal life.

For my thesis, I determined what the effects of redcedar encroachment are on both the physical and biological environment within Cross Timbers forests of central Oklahoma. This work is divided into two separate studies that both focus on species biodiversity.

The first study examined the effects of redcedar on the physical environment of the Cross Timbers forest (i.e., soil moisture and chemistry, microclimatic attributes, and understory light environment, and how these changes influence the understory plant community). In addition to determining species richness, species composition and plant cover, regression analysis and partial Canonical Correspondence Analysis (pCCA) were used to establish relationships between vegetation variables and differences in the physical environment. This allowed me to determine how redcedar encroachment mediates changes in understory vegetation. The study design involved ten sites, each with four sampling points distributed over five different treatments representing a cline of increasing woody and redcedar cover.

The second study focused on the effects of the development of a redcedar midstory on wintering avian community in the Cross Timbers. Through mist netting, I was able to determine the physical condition of several wintering bird species. A body condition index was calculated using Principal Component Analysis (PCA) on various body measurements. This allowed me to compare body conditions between birds caught in redcedar-encroached forests and birds captured in oak-dominated Cross Timbers. I also performed 500 m long transect counts during two consecutive winters (2007—2008/2008—2009) to establish the presence of temporal variation in bird community composition. In addition, point counts were performed to establish the relationship between bird species and redcedar density.

Alterations in both bird and plant communities due to redcedar encroachment in the Cross Timbers forest are illustrative of the profound influence of fire suppression on community dynamics and ecosystem function. Similar effects of redcedar encroachment on other taxa occur as well, especially those that are ecologically linked directly to understory vegetation or bird life. These two studies represent an important picture of what happens to biodiversity in the Cross Timbers forests during redcedar encroachment and are important contributions to the growing knowledge base on ecological effects of the spread of eastern redcedar.

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CHAPTER II

REVIEW OF LITERATURE

GENERAL CHARACTERISTICS OF *JUNIPERUS VIRGINIANA*

Eastern redcedar (eastern red cedar, eastern juniper, savin, *Juniperus virginiana* L.) is a coniferous tree of the genus *Juniperus* (Cupressaceae) that includes 52 (Farjon 2001) to 67 (Adams 2004) species. The species grows to 30 m high, but usually does not grow taller than 10 m and in places with adverse growing conditions this tree only reaches shrub size. At ground level, the diameter of the trunk rarely exceeds 50-100 cm (Kent 1900). The record redcedar has a height of 37 m and a Diameter at Breast Height (DBH) of 122 cm (Lawson 1986). The trunk of *J. virginiana* is usually irregularly shaped in cross-section (Lawson 1986). The bark of redcedar is distinctly thin, has a light brown color and peels off easily (Kent 1900). Wood characteristics of redcedar include red heartwood and white sapwood (Lawson 1986). The heartwood is resistant to damage such as rot, fungi, and insects (Schmidt and Kuhns 1990). However, minor fungal infections can occasionally occur in the heartwood (Hepting 1971). It is a mostly dioecious tree, although monoecious populations of the species have been found. There are morphological differences between the two sexes; these include branching patterns (males have stiffer branches) and leaf color (males in winter russet-brown, females green year-round) (Kent 1900).

Leaves show morphological differences between juvenile and mature ages (Kent 1900). At the juvenile stage, leaves are opposite, about 3 mm long and have a distinct needle-like shape. Juvenile leaves can be retained for a few years, and can even persist along with mature leaves (Harlow and Harrar 1969). Mature leaves are most often opposite or ternate; they overlap and have an acute tip. Mature leaves look like scales and have entire margins. They are as long as juvenile leaves and usually are a darker green (Van Haverbeke and Read 1976). Most authors (Kent 1900, Harlow and Harrar 1969)

consider *Juniperus virginiana* to have dimorphic leaves, but Van Haverbeke and Read (1976) recognize a third type of leaf, which occurs in shoots during periods of rapid growth and has an elongate shape. Leaves of the species usually stay on the tree for five to six years (Collingwood 1938). Eastern redcedar strobili are either staminate or ovulate (given their generally dioecious nature) and are generally produced only by trees which are ten years old or older. Female trees produce ovulate strobili which have a berry like appearance, but are in fact cones (sometimes called conelets). Non mature ovulate strobili usually contain two seeds, occasionally up to four or more. These strobili start to develop at the end of the summer or beginning of fall and ripen slowly during the winter season until they spread seeds from February through early spring. In June, fertilization occurs, and ovulate strobili turn from green, through white to a dark blue color. Male or staminate strobili are formed in September, when ten to 12 sporophylls are produced within the cone (Johnsen and Alexander 1974, Van Haverbeke 1985).

Seed production in eastern redcedar occurs every year, but mast years only occur every two or three years. Cones do not open up and stay on trees during the entire winter. Many cones are eaten by frugivorous birds and mammals (Halls 1977, Horncastle et al. 2004) during the winter season and the remainder is dispersed by the tree in February and March (Van Haverbeke 1985).

The rooting behavior of redcedar has been well studied by various authors. The species produces a fibrous root system during its seedling stage, but upon maturing starts developing a taproot (Fowells 1965, Ferguson et al. 1968, Hinckley et al. 1979). This characteristic is variable, however, and depending on soil type redcedar retains the fibrous root system throughout maturity or replaces it with a tap root. On rocky soils and in areas with a shallow ground water level for example, taproots are often not formed (Mohr 1901, Bunger and Thompson 1938, Bannan 1942, Arend 1950, Williamson 1965, Spracking and Read 1979). Eastern redcedar is one of the most widely distributed juniper species of the world. Its native range spreads from the Canadian province of New Brunswick down along the United States East coast to northern Florida and thence to central Texas. In the central United States, it is found northwest to central South Dakota (Petrides and Wehr 1988). The species is commonly planted in many areas as a windbreak or ornamental tree, which has stimulated its spread, especially in the Great

Plains states of the United States (Van Haverbeke and Read 1976) and even outside North America, for example in central Asia (Rubanik and Zeronkina 1969), where the species is not native. In Oklahoma, redcedar spread throughout the Panhandle and extreme southwestern corner of the state between 1985 and 1994 (Snook 1985, Engle et al. 2000), areas which were formerly strongholds of other species of juniper (*J. ashei, J. pinchotii, J. monosperma, J. scopulorum*).

Eastern redcedar persists within its wide range in many different climatic areas. Annual precipitation within the range of *Juniperus virginiana* varies from 380 mm to 1520 mm. Average snowfall per year within the range varies from none to 254 cm. Average annual temperatures range from 4°C in the north to 20°C in the south. The lowest average minimum temperature within the range is -43°C and the highest average maximum temperature is 41°C. The growing season within the range is from 120 to 250 days (Williamson 1965, Lawson and Law 1983).

J. VIRGINIANA IN THE PRAIRIE BIOME

A large part of the distribution of eastern redcedar falls within the native North American grasslands, which stretch northwest from Illinois to the Canadian province of Ontario, and south to western Texas and central Oklahoma. Redcedar has recently invaded large parts of the prairie biome where the species was formerly largely absent, mainly due to a combination of planting as a windbreak or ornamental species and fire suppression (Owensby et al. 1973). The spread of *J. virginiana* occurs not only in native North American grasslands, but also in rangelands and especially abandoned fields (Ormsbee et al. 1976, Lawson 1986).

Fire is the most important factor for the natural suppression of redcedar in many prairie areas (Owensby et al. 1973). Redcedar naturally occurred areas within the prairie biome where fire was naturally absent, because of a low fine fuel (grasses) production in the rocky landscape surrounding rivers (Snook 1985). Poor soils and rocky ridges have been indicated as the major historical growth sites for the species, due to the absence of wildfires in these places (Harper 1912, Burkhardt and Tisdale 1976). However, in the absence of fire, redcedar first invaded fertile lowland sites whereas dry upland sites were colonized last (Bragg and Hulbert 1976). The reason that redcedar is susceptible to fire

damage is that the thin bark and surface roots are a good fuel (Ferguson et al. 1968) and redcedar does not resprout if the top is burned (Arend 1950). Moreover, volatile oils in the foliage are highly flammable.

In Oklahoma, the grassland areas most affected by the spread of redcedar are the grasslands of the central western counties, such as Caddo, Comanche, and Woodward (Engle et al. 2000). In the absence of fire, native grassland can convert into a closed-canopy redcedar forest within 40 years (Briggs et al. 2002a). Redcedar biomass can be reduced by the reintroduction of fire (Bragg and Hulbert 1976).

Fencing and the absence of grazing can also increase the redcedar incidence in grasslands, as seedling survival is more likely in these cases (Schmidt 1991). The impact of grazing on seedlings is twofold; grazing effects on redcedar occur through compaction of the soil and through direct predation of the plants. However, the invasion of redcedar apparently cannot be completely prevented by introducing livestock; only a reduction in invasion rates is possible (Owensby et al. 1973). Schmidt (1991) found no evidence of redcedar grazing by cattle. Sheep and goats, however, will graze redcedar seedlings (Fitter and Jennings 1975). Grazing can also decrease fuel stocks, thereby reducing fire, and increasing abundance of woody species, including redcedar (Briggs et al. 2002a, Briggs et al. 2002b).

Redcedar has been, and still is, a particularly quick colonizer of abandoned fields (Ormsbee et al. 1976, Lawson 1986), where, similar to native grassland in insolation and cover, redcedar is benefited by the prevailing microclimatic conditions. Ormsbee et al. (1976) observed that redcedar needles did not light saturate even at 1750 μmol $m^{-2} \cdot s^{-1}$ and the optimum photosynthetic temperature lay around 20°C. Redcedar in open situations can photosynthesize in winter on mild days, and in summer during periods of intense solar stress.

J. VIRGINIANA IN CROSS TIMBERS FORESTS

Although not as well known as the spread of redcedar in the prairie biome, the transitional forests between the prairie and eastern forest biomes of the Cross Timbers ecoregion have seen a marked increase of redcedar over recent decades. Eastern redcedar has always been present in small numbers and on infertile sites throughout the Cross

Timbers (Therrell and Stahle 1998). However, a comparison of data from as recent as 1985 and 1994 indicates that redcedar has become more abundant in several counties within the Cross Timbers ecotype in Oklahoma, such as in the counties surrounding Oklahoma City (Logan, Lincoln, Pottawatomie, McClain) and in other counties of central Oklahoma such as Okmulgee (Snook 1985, Engle et al. 2000).

Redcedar encroachment in the Cross Timbers occurs for similar reasons as in the native grasslands: the absence of fire (Engle and Stritzke 1995, Therrell and Stahle 1998). Historically, redcedar was found within the Cross Timbers only at sites which did not burn, such as in isolated rocky areas (Therrell and Stahle 1998). Redcedar invasion can be minimized through regular use of prescribed fire. In particular, the use of fire in fall after natural leaf fall by overstory trees, which creates a good fuel bed, will kill redcedar. The combination of an herbicide (e.g., tebuthiuron) and prescribed fire seems the most effective combination to reduce redcedar numbers, because the herbicide increases leaf litter on the forest floor, which acts as a fuel bed. However, this method also kills a proportion of the overstory trees in a Cross Timbers forest and defeats the purpose if used solely to remove redcedar from a forest (Engle and Stritzke 1995).

Redcedar thrives in a high light environment, however trees can survive for decades under dense overstory cover of hardwood species or *Pinus* spp. on poor soils. In Missouri, redcedar often grows well in oak-hickory forests as an understory species under less than 10% of incident light (Lassoie et al. 1983). However, several authors report that the species is intolerant of shade (Ferguson et al. 1968, Ormsbee et al. 1976). Seedlings of redcedar on the contrary are tolerant to shade according to Beilmann and Brenner (1951), a characteristic they need to survive under dense grass or tree cover (Smith 1986).

In forests, hardwood species usually are taller than redcedar; the latter is generally restricted to subcanopy and lower forest strata. In large parts of its range, eastern redcedar is associated with pines (*Pinus* spp.), hickories (*Carya* spp.) and black walnut (*Juglans nigra*) (Eyre 1980). In the Cross Timbers, redcedar occurs with a variety of oak species, mostly post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*), but also chinquapin oak (*Q. muehlenbergii*). Other associated woody species include chittamwood (*Sideroxylon lanuginosum*) and smooth sumac (*Rhus glabra*). Some of the graminaceous

species in the prairie biome, also occur in the Cross Timbers, often in close vicinity of redcedar (Eyre 1980, Francaviglia 2000).

EFFECTS OF *J. VIRGINIANA* ON SOIL PH

Soil pH influences growth of plants as most plant species only grow within a certain range of pH, and any alterations in soil pH can limit growth or even exclude particular plant species. Changes in soil pH also can affect soil nutrient status by altering the chemical composition of the soil. Detritivore activity and the decay of leaf litter are also linked to certain pH ranges and may change with any reductions or increases of soil pH. Soil pH indirectly influences plant growth as soil nutrients, detritivore activity and leaf litter dynamics are all important factors that alter growing conditions for plants.

Dead leaf matter of most coniferous trees has an acidifying effect on soils (Hesselman 1917, Němec and Kvapil 1926, Alway et al. 1933). Conifer leaves contain high levels of tannic acid (Hernes and Hedges 2004) and in general have a lower pH than foliage of deciduous species. However, redcedar contains a large amount of cations in its leaves and therefore has a buffering effect on soil acidity, raising pH of acidic soils. (Lutz and Chandler 1946, Coile 1933, Spurr 1940, Read and Walker 1950, McBain 1983). One study found that soils under redcedar stands had an average pH of 6.7 compared to pH 6.0 for soils under six other forest types (Coile 1933). In general, the capacity of litter to buffer soil pH is greatest in the upper soil layers whereas deeper soil layers remain fairly acidic (Doyne 1935). The buffering effect of redcedar was greatest in the humic layer, with an average of pH 7.0, compared to an overall average of pH 6.0 for seven other forest types. As depth increased, soil pH under redcedar decreased to 6.7 in the first 5 cm of the mineral soil and to 6.3 at a depth of 40-45 cm. In contrast, pH under post oak-blackjack oak forest type ranged from 4.1 for the litter layer to 6.0 at 40-45 cm deep (Coile 1933).

The buffering effect of redcedar foliage on soil pH can be diminished by the presence of other trees with higher folic acid contents. In a study from eastern Nebraska, which included redcedar as a component of a shelterbelt with Scots pine (*Pinus sylvestris*), average soil pH values were lower than those of surrounding fields. Soil pH values under the shelterbelt ranged from pH 5.5 to 6.7, compared to 6.1 to 6.9 for the

fields. The shelterbelt values were lower than values found in other studies of soil pH under redcedar because Scots pine had an acidifying effect that exceeded the buffering effect of redcedar (Sauer et al. 2007).

On soils with naturally high pH, such as calcareous prairie soils, redcedar litter does not raise pH levels. These soils generally have higher pH values than redcedar leaf litter such that redcedar in this case can acidify soils. Prairies in Louisiana that were overgrown with redcedar had an intermediate soil pH between the high pH levels of calcareous prairie and forests dominated by more acidifying species (Bekele et al. 2006). The same is true for savannas in Pennsylvania, which occur on serpentine soils with a naturally high pH. Savannas that are invaded by eastern redcedar have lower soil pH values and exchangeable calcium than savannas where redcedar is absent (Barton and Wallenstein 1997).

A different source of acidification of soils than litter inputs is acidic stem flow and throughfall. It has been determined for oaks (*Quercus* spp.) that their leaf litter acidifies soils, but soil pH was also consistently lower around the tree bole than farther away from the tree (Leonora and Reich 1993). The effects of redcedar on stem flow and throughfall have yet to be determined.

EFFECTS OF *J. VIRGINIANA* ON SOIL WATER

Soil water status can be influenced by trees in several ways; before precipitation can enter the soil and become available for plant use it must first pass through the canopy and litter layer. Precipitation intercepted by the canopy can run down the stem of the tree (stem flow), run off the branches of the tree (drip, throughfall), or evaporate from the branches and foliage into the air (Rowe and Hendrix 1951). Stem flow has a dramatic effect on the spatial distribution of water because water runs from outer branches to the center of the tree, thus concentrating moisture around the tree bole (Martinez-Mena and Whitford 1996, Devitt and Smith 2002). This can result in a ratio of water concentration of 21:1 directly around the bole proportional to other areas, as in the case of Ashe juniper (*J. ashei*) on the central Texas Edwards Plateau (Moore and Owens 2006). That which does not evaporate from the canopy must then pass through the litter layer which absorbs a portion of the precipitation, but also moderates the percolation of water into the soil and

prevents overland flow. Therefore, stand structure is important to water availability because of the influence of stand and canopy density on canopy interception (and evaporative losses) as well as spatial distribution of soil water.

Interception of water by tree canopies is species specific. Important factors are leaf morphology and foliage quantity (Owens 2008). Leaf area is positively correlated with interception and evaporative losses. Coniferous species, which generally have a higher Leaf Area Index (LAI), often intercept more precipitation and interception can reach 48% of total rainfall (Carlyle-Moses 2004). Ashe juniper, which is similar in morphology to eastern redcedar, intercepted large amounts of moisture because of its leaf morphology (scale-like leaf structure and high LAI) (Owens 2008). Interception can either lead to higher soil moisture through greater retention of water by branches and gradual leaching into the ground (throughfall), or to lower soil moisture, if water is evaporated that normally would have infiltrated the soil (McBain 1983).

Some studies indicated that soil moisture under redcedar is greater than under herbaceous vegetation in native prairies, while others have shown the opposite. In a study from north central Mississippi (Broadfoot 1951), soil under redcedar contained 10% less soil moisture than under grasses or legumes. McBain (1983) found similar results on three different sites, one in which redcedar was present and the other two in which redcedar had recently been removed. In a study from Tennessee, soil moisture under redcedar cover varied strongly across seasons. The soil is driest in summer and restricts herbaceous plant growth because soil water potentials decrease below wilting point. Springtime is usually the wettest and there is sufficient soil water for plant growth (Freeman 1933). In drier regions, *Juniperus* spp. also may decrease soil water. Angell and Miller (1994) found that western juniper (*J. occidentalis*) was able to deplete the abundant spring soil water supplies, thereby reducing availability of soil water for herbaceous species. In contrast to the above mentioned studies, Emerson (1932) found that soil water was four times more available under a pinyon-juniper dominated forest than under adjacent grasslands. Junipers including redcedar seem to have different effects on soil water status, depending on site conditions and climate.

Compared to deciduous trees, redcedar differs in its ability to transpire during dry conditions and in the timing of seasonal water use. *Juniperus* species keep their stomata

open and transpire water even when soil conditions are extremely dry. Furthermore, because junipers are evergreen trees, they use available soil water year-round (Angell and Miller 1994). Redcedar is adapted to xeric conditions given the fact that the species is able to photosynthesize at low xylem pressure potentials (below -3.2 MPa) (Ormsbee et al. 1976, Bahari 1981, Lassoie et al. 1983). Redcedar saplings have lower leaf conductance than most angiosperms, which results in lower rates of leaf-specific water loss (Bahari 1981). Only during the hottest days in late summer did redcedar close stomata, reducing water loss and photosynthesis to 30% of the levels found during other times of the year (Lassoie et al. 1983). Other species in comparative studies show stomatal closure during cold weather and sooner than redcedar during the warm season dry-periods (e.g. *Sassafras albidum, Ulmus alata, Diospyros virginiana* (Ormsbee et al. 1976). Redcedar, unlike most species of angiosperms, has the ability to store water in apoplastic spaces in the xylem when the tree is experiencing water stress, delaying the decline in leaf water potential. In most angiosperms, this happens through storage of water in leaf intercellular spaces (Bahari 1981).

In a study comparing soil water potential around redcedar at two different depths (15 cm, 90 cm) (Ginter-Whitehouse et al. 1983), soil water potential was especially low in the upper 15 cm of the soil, indicating that redcedar uses mostly water from upper soil layers. Two other species in the study, black walnut (*Juglans nigra*) and white oak (*Quercus alba*), extracted more water from the soil than redcedar due to more extensive root systems and higher transpiration rates. Emerson (1932) found that transpirational losses from a pinyon-juniper community are about equal to those from a grama dominated community when the woody species are immature. However, when the woodland community gets older and has more leaf area, transpirational losses increase compared to grasslands and can be up to four times greater. Furthermore, it has been shown that redcedar in open stands (e.g. in a savanna) transpire more than those under a canopy of other species or older specimens, because of a combination of increased LAI in open stands and more influence from wind and sun (Owens 2008).

Tree cover can also reduce soil moisture through root systems. Root systems create soil macropores, and leave a permeable soil structure after decay. This increases soil hydraulic conductivity, as larger pores more easily let water flow to greater soil

depths. A study for redcedar specifically shows that average macro-pore volume increases in soils under redcedar compared to soils under herbaceous cover or pines (Read and Walker 1950). This means that water can more easily enter soils under redcedar and more easily penetrate deeper soil layers. Even though some mature redcedar individuals develop tap roots, the species' root systems are generally shallow and they take up most soil water from upper soil layers. However, in case of drought, redcedar seedlings develop a quick-growing tap root, which is able to take up water from deep soil layers, often at the expense of aboveground growth (Kramer 1949).

EFFECTS OF *J. VIRGINIANA* ON SOIL TEMPERATURE

Soil temperature is important to consider in relation to productivity of trees and herbaceous vegetation. With higher soil temperatures during the cold season, plants are able to start growth earlier in spring (spring annuals), whereas during the summer, lower temperatures may reduce soil moisture limitations through lower evapotranspiration. Soil temperature may also have an important effect on mineralization and decomposition rates through changes in detritivore activity. All studies show a decline in soil temperature with increased cover of trees, due to less incoming solar radiation (Tiedemann and Klemmedson 1977, Everett and Sharrow 1985, Pierson and Wight 1991, Breshears et al. 1998, Chambers 2001). Soil temperature is also consistently lower on the north side of a tree than on the south side of the tree (all studies being from the northern hemisphere), due to southern sun exposure and shading on the north side of the tree. Lower solar radiation at the soil surface reduces evaporation and increases soil moisture which further moderates soil temperature. Also, due to lower temperatures, litter accumulation is higher, which also further decreases solar radiation reaching the mineral soil (Tiedemann and Klemmedson 1977, Breshears et al. 1998). Throughout the soil profile, soil temperature is highest in areas without tree cover, intermediate with only shrub cover and lowest with tree cover (Tiedemann and Klemmedson 1977, Everett and Sharrow 1985, Breshears et al. 1998, Chambers 2001). However, at greater soil depths (15 cm and 30 cm) seasonal and daily temperature fluctuations are less marked. In one case under honey mesquite (*Prosopis glandulosa*), differences between wooded and grassland ecosystems occurred during the summer, but not the winter (Tiedemann and Klemmedson 1977).

A study from Japan found that underneath trees with an erect-type canopy, which include most coniferous trees, maximum and minimum temperatures are on average more extreme than underneath trees with prostrate-type canopies, which include most deciduous trees. This is true regardless of differences in LAI (Duangpaeng et al. 2002). Given the variable morphology of eastern redcedar crowns, it is unclear what effects redcedar canopy cover has on soil temperature when compared to deciduous forest.

EFFECTS OF *J. VIRGINIANA* ON SOIL NITROGEN

Nutrient availability, in particular nitrogen availability, is important for ecosystem functioning, because it is a major determinant of plant growth and productivity. Species like eastern redcedar can have a profound effect on soil nutrient status through rapid growth and subsequent accumulation of tree biomass. The maintenance of higher biomass accumulation rates in redcedar is accompanied by higher nutrient uptake from the soil, leading to comparatively less availability for competing species (Chapin 1980, Vitousek 1982). Changes in plant litter quantity or quality also affect soil nutrient status because litter is a key component of the nutrient cycle. Much of the plant available nitrogen is associated with foliar litter inputs and root turnover or exudates (McClaugherty et al. 1982). Soil nitrogen levels are for this reason intimately linked to activity of the soil O horizon. In one study from the Flint Hills of Kansas, redcedar produced on average 504 $g.m^{-2}.y^{-1}$ litter. Of this litter about 4.11 $g.m^{-2}$ was nitrogen resulting in annual inputs of 25-56 $g\ N.m^{-2}$ (Norris et al. 2001a, McKinley 2006). Sauer et al. (2007) reported that 74% of the litter nitrogen found in a redcedar-Scots pine shelterbelt was located both in the deeper duff layer, characterized by fine texture (47.4 $kg\ N.ha^{-1}$) and in the shallow duff layer, characterized by coarse texture (16.7 $kg\ N.ha^{-1}$), with an additional 26% on top of the duff in fresh leaf litter.

Average nitrogen concentration in the aboveground biomass of redcedar was 0.40%. Concentrations by component were 1.09% for foliage, 0.65% for bark, and 0.25-0.34% for live branches (Norris et al. 2001a). Temporally, the highest concentrations of nitrogen were found in redcedar foliage in mid-growing season (July) with C:N ratios measured of 37:1. This is similar for other plant species, such as grasses, which had a average C:N ratio of 56:1. Just before senescence these two numbers increased to 52:1

and 70:1 respectively, as nitrogen was translocated (McKinley *et al.*, 2008). In a study focusing on a mixed redcedar-Scots pine system, soil nitrogen was approximately 350 $g.m^{-2}$ (Sauer et al. 2007).

In a comparative study between native North American grasslands and redcedar forests, the concentration of nitrogen in redcedar fine roots was 0.74% versus 0.51% in fine roots of mixed species in grasslands (McKinley 2006). However, another study comparing these numbers for eastern redcedar and big bluestem shows the opposite (Norris et al. 2001a). This difference may be attributed to temporal or site-specific variation or may even be due to selection of different sized roots in the two studies according to McKinley et al. (2008). Norris et al. (2001b) found that redcedar roots decay 35% slower than roots of big bluestem. This means that redcedar contributes more to the accumulation of soil organic matter than big bluestem which increases soil nitrogen levels, but may reduce plant available nitrogen. Net immobilization rates in this study were high in both redcedar and bluestem litter, thus preventing most N from being accessible to plants. Root inputs of N in redcedar have not been well studied and there may be an important role for belowground litter inputs in nitrogen cycling (McKinley et al. 2008). If we consider the ecosystem as a whole, 85% of the nitrogen found belowground in a native prairie remained belowground in a redcedar invaded prairie (Smith and Johnson 2003, McKinley 2006).

As discussed above, the inputs of plant available nitrogen are important for plant growth. However, in the short run, the net release of nitrogen (mineralization) from decomposing redcedar litter is slow. No mineralization of nitrogen was detected from redcedar litter in a two-year study period (Norris et al. 2001a). McKinley (2006) found similar results over a shorter period of time. There are no data available for root decomposition (McKinley et al. 2008).

There are several comparative studies that contrast redcedar soil nutrients with soil nutrients under a native North American grassland. Some of these (Norris et al. 2001a, McKinley 2006) point out that grassland total N stores are much lower than stores in redcedar stands due to fire. Fire volatilizes a portion of total system nitrogen and grasslands in general burn more frequently than forests. Frequent fires can reduce system nitrogen in the long run through repeated volatilization losses combined with relatively

low fixation rates. Redcedar stands are on average 2.5 times more productive in terms of aboveground net primary productivity (NPP) than grasslands and show double the nitrogen use efficiency (NUE) compared to native grasslands (Norris et al. 2007). Given that redcedar aboveground biomass continues to increase each year while aboveground biomass of herbaceous plants either dies each year and/or burns, much more nitrogen accumulates in biomass of a redcedar stand than in biomass of a grassland. This means that in the absence of fire, which is usually the case for a redcedar stand, more nitrogen is held in biomass, whereas in grasslands which are frequently burned, nitrogen is regularly released and does not have a chance to accumulate in biomass (Norris et al. 2001a, McKinley 2006).

Variations in soil nitrogen within juniper stands also have been established, with subcanopy sites having greater nitrogen turnover and greater plant available nitrogen content than intercanopy sites (Padien and Lajtha 1992). Contrastingly, McBain (1983) found no significant differences in total soil nitrogen between redcedar subcanopy, edge of canopy and native grassland sites. A significant buildup of organic matter was found around the tree bole. Klopatek (1987) showed that a 35-year-old pinyon-juniper forest had lower soil nitrogen availability than an old-growth forest of 300-400 years of age. This difference is probably due to greater disturbance in the younger sites, coupled with nitrogen stores disappearing from the ecosystem. Interestingly, this author also found no difference in soil nitrogen availability between subcanopy and intercanopy sites. However, nitrogen mineralization rates were higher in intercanopy than in subcanopy sites, yielding higher levels of plant available nitrogen in intercanopy sites.

EFFECTS OF *J. VIRGINIANA* ON LEAF LITTER ACCUMULATION

Litter accumulation has a profound effect on soil attributes and understory plant dynamics. As discussed above, the soil mineral nutrient status can be altered by litter. This is particularly important for soil nitrogen and phosphorus. Also, leaf litter in some plant species has the ability to change the soil pH as well as the potential to change soil water status through various mechanisms. Litter reduces light intensity and light quality (more light from far red spectra than red spectra (Vázquez-Yanes et al. 1990)) reaching the mineral soil to and may have an important negative effect on seed germination. Leaf

litter also acts as a mechanical barrier for plants and especially recently germinated seedlings. Small seeds in some cases have energy reserves that are too low to break through a thick litter layer. Larger seeds can be inhibited from germinating by increased fungal infections or herbivory under a think layer of dead leaf matter. Other seeds do not receive sufficient energy to transition from the dormant phase (Facelli and Pickett 1991). The mechanical barrier effect of leaf litter is greater in species that produce leaves that grow vertically through the litter layer than for species that grow from a basal meristem (Sydes and Grimes 1981). Lastly, litter can have an effect on soil and plant life through phytotoxins present in the leaf matter of certain plant species that have an allelopathic effect. The exact mechanisms by which this happens have not been well studied in the field and presumed phytotoxic effects are often confounded with other factors that limit plant germination or growth (Facelli and Pickett 1991).

One study focusing on xeric longleaf pine woodlands (*Pinus palustris*) with a developed *Quercus* sp. midstory in Florida found that litter accumulation was the primary driver behind reductions in understory plant productivity and diversity. In absence of a fire, litter accumulation was higher than in pine woodlands (that were regularly subjected to fire) and was negatively related to herbaceous productivity and diversity. While light reaching the understory also decreased with the development of the midstory, irradiance was not directly related to the understory (Hiers et al. 2007). Other studies also show that fire can have an important effect on understory vigor through litter depth reductions (e.g. Facelli and Pickett 1991).

Compared to other species redcedar produces large amounts of relatively decay resistant litter. Redcedar produces about 500 $g.m^{-2}.y^{-1}$ litter (Norris et al. 2001b), whereas this number for native grasslands is almost 10 times smaller (52 $g.m^{-2}.y^{-1}$). Most of this litter is produced during late summer and fall, when water availability is lowest. During spring, little litter is produced by redcedar. Redcedar litter contains little woody components, due to the fact that redcedar does not self-prune. Redcedar does, however, have fairly high lignin content. Lignin to nitrogen ratio for redcedar leaf litter is 10:11. The decay rate of redcedar litter in forest habitat is 32.1% per year. The decay rate for the prairie grass *Andropogon gerardii* is 41.5% (Norris et al. 2001a). This higher number can be explained by the higher lignin to nitrogen ratio in redcedar. Also, needles generally

need a longer time to decay than leaves of deciduous trees, due to the effect of higher lignin content in the structurally smaller but tougher conifer needles, as well as a possible effect of tannins that deter folivores (Cornelissen 1996). Dye II *et al*. (1995) found that *Juniperus pinchotii* litter covered almost the entire forest floor directly around the base of the tree (92-97%) whereas this number is lower, but still fairly high halfway between trunk and crown edge (82-90%). The mass of accumulated redcedar leaf litter (including duff layer) in redcedar stands in the Flint Hills, southeastern Kansas, was approximately 1628.2 $g.m^{-2}$, whereas litter in nearby grasslands was nearly absent (Norris et al. 2001a).

Various authors have shown than redcedar leaf litter has the potential to raise pH of the top soil (Coile 1933, Spurr 1940, Read and Walker 1950, McBain 1983). Because of its almost neutral pH (average pH of 6.4; (Coile 1933), redcedar leaf litter creates favorable conditions for soil invertebrates such as earthworms, which rapidly turn leaf litter into soil organic matter with a lower weight per volume and a higher pore space (Read and Walker 1950). The sharp demarcation line that usually exists between humus of other coniferous trees (with more acidic leaf matter) and the mineral soil is absent in soils under redcedar, because of increased mixing of the two due to increased soil invertebrate activity (Coile 1933).

Decreased herbaceous production beneath redcedar could be caused by allelopathic effects of leaves or roots (McBain 1983, Engle et al. 1987). A related species (*J. osteosperma*) (Jameson 1966, 1970a) contains allelopathic substances. One experimental study indicated that there were no significant allelopathic effects on grass growth related to redcedar duff. Four native North American prairie grasses were subjected to redcedar duff applications. Rather than a negative effect of the duff, grass grew faster in winter and summer due to the application of redcedar duff and had higher than normal weights. However, germination was slightly reduced in long-lived perennial species (Smith 1986). In a study with five herbaceous species, one showed reductions in germination success after being planted in soil collected around redcedar. The authors of the study add that it is yet to be confirmed whether or not allelochemicals from redcedar prevent seed germination of herbaceous species or if allelopathy just delays germination (Stipe and Bragg 1988).

EFFECTS OF *J. VIRGINIANA* ON VAPOR PRESSURE DEFICIT

Atmospheric water vapor is usually referred to as humidity. Humidity can be described in absolute or relative terms. Absolute humidity describes the actual weight of water per unit volume of air. Relative humidity is the percentage of water present in the air relative to the maximum water holding capacity of the air. The water holding capacity of air increases exponentially with temperature. Vapor pressure deficit (VPD) is used to standardize the evaporative demand that drives evapotranspiration. Vapor pressure deficit (measured in Pascals) is the difference between the vapor pressure in the intercellular air space (assumed to be fully saturated) and the vapor pressure of the ambient air (Spurr and Barnes 1980).

VPD in forests influences different ecosystem components. Firstly, there is a link between VPD and stomatal opening or closure in plants. If stomatal conductance does not change, transpiration is a direct function of VPD. However, stomata respond to VPD and generally decrease as VPD increases, perhaps to limit water loss. When the air is saturated with moisture, however, vapor pressure in the intercellular air space may be lower than the surrounding air and may cause water to enter the plant through the stomata. In these ways, humidity, and resultant VPD can have both a positive and a negative effect on plants (Spurr and Barnes 1980). It has been shown for Ashe juniper (*J. ashei*) on the Edwards Plateau of central Texas that high humidity after rains reduce transpiration, but that levels of transpiration similar to before the rain event were reached again only 90 minutes after the rain stopped (Owens 2008).

The reduction in transpiration caused by higher atmospheric humidity has positive effects on plant growth. Low VPD contributes to greater fruit weight and water content in tomatoes (*Lycopersicon esculentum*) grown in greenhouses (Leonardi et al. 2000). Summer and its more intense solar radiation cause VPD to go up, and fruit weight to go down. Likewise, lowered VPD and reductions in transpiration and resultant water stress could positively affect understory plants in a redcedar-dominated area.

There are several factors that contribute to higher humidity in forest understories. Evaporation from soils and transpiration from understory plants are important factors in raising air humidity under canopies (Powell and Bork 2007). Precipitation and water conductance by stems and branches also add to understory water vapor. Forest canopies

retain humidity in the understory atmosphere. The denser forest canopies, the more water is held in the understory atmosphere, due to a combination of retention of humidity in the understory and a lack of air perturbations. Coniferous trees because of their high LAI usually have lower VPD in the understory compared to deciduous trees or open conditions (Molga 1962). Porte et al. (2004) observed a strong effect of forest cover on relative humidity and VPD. However, significant differences between different aged stands and humidity or VPD were not found. Edge-effects exist as well; areas farther away from edge have lower VPD. Harvesting of trees and the subsequent creation of clearings increases VPD. This is partly due to exposure to sunshine, which increases temperature and VPD.

VPD within forests fluctuates in time. At night, forest clearings have lower VPD than closed forest understory due to greater cooling in the gaps. During a drought, such as often occurs in summer in many areas, VPD is lower under full or partial cover of trees. With precipitation, there is generally no difference between clearings and closed canopy areas (Powell and Bork 2007). MacHattie (1966) found that the influence of precipitation on relative humidity in mountainous forests of southern Canada lasted only a day on average (MacHattie 1966).

EFFECTS OF *J. VIRGINIANA* ON THE LIGHT ENVIRONMENT

Light energy, (i.e. photosynthetically active radiation), is an essential for growth in all green plants. Photosynthetically active radiation (PAR) is defined as light in the spectral range of 400-700 nm. Absence or reduction of light levels underneath a dense tree canopy can reduce or even exclude herbaceous plant species. Smith (1986) reported an 85% reduction of PAR under redcedar compared to under grasses in a nearby native grassland in Nebraska. This sharp reduction in light levels is caused by the greater LAI of redcedar relative to that of the grasslands and due to the planophile canopy arrangement of redcedar. Redcedar as a midstory component in combination with a hickory-dominated overstory in a forest in Missouri let through only 10% of the above canopy light levels (Hinckley et al. 1981).

Van Pelt and Franklin (2000) found that for old-growth coniferous forests there was no correlation between understory light conditions and the canopy structure directly

above. This is probably caused by the constantly changing sun angle which causes horizontal shifts between light penetration and canopy position. The authors therefore conclude that LAI is a poor predictor of light conditions in the lower strata of the forest. However, these authors use data from old-growth forests of the Pacific Northwest of the United States, which are probably of higher stature than most redcedar stands, and the horizontal shifts probably do not play a similarly important role in redcedar.

An additional light reducing effect can be attributed to the litter layer. In North American grasslands, litter can intercept between 95 and 99% of incoming radiation (Knapp and Seastedt 1986). Litter also changes the quality of light because different types of litter have different types of extinction coefficients (Facelli and Pickett 1991). This may have an important impact on seed germination and seedling survival below the litter layer.

EFFECTS OF *J. VIRGINIANA* ON HERBACEOUS VEGETATION

Redcedar influences herbaceous species in a number of ways. Dense cover associated with redcedar and many other coniferous trees can prevent light and precipitation from reaching the forest floor. Junipers are known to reduce light availability on the forest floor level by up to 80% (Jameson 1970b). The relatively high amount of leaf litter produced by dense canopies can cover the forest floor and prevent seedlings from germinating and young plants from reaching light (Anderson et al. 1969). Redcedar can also affect herbaceous vegetation by altering the soil characteristics (pH, nutrient availability) where the species grows (Bekele and Hudnall 2005). Redcedar increases soil pore volume through root die-off. Because it has larger diameter roots than those of forb or grass species, soil water movement to deeper soil layers may increase and water availability in the upper soil may decrease (Kittredge 1938). Redcedar roots compete directly with roots of forbs and grasses for available water and soil space (Jameson 1970b).

There are several studies of redcedar effects on herbaceous vegetation in the prairie ecosystem (Engle 1985, McPherson and Wright 1990, Gehring and Bragg 1992). Gehring and Bragg (1992) found that redcedar alters the herbaceous species composition by preventing precipitation from reaching soil. They concluded that the native herbaceous

vegetation was reduced in favor of the non-native Kentucky bluegrass (*Poa pratensis*) and *Carex* spp. These both showed an increase in cover under redcedar compared to areas without redcedar cover. At the crown-edge of redcedar, little bluestem (*Schizachyrium scoparium*) and big bluestem (*Andropogon gerardii*) increased compared to directly underneath the tree; however Kentucky bluegrass was still present. Outside of the direct shade area of redcedar, native grasses such as little and big bluestem dominated, and native forbs such as white aster (*Symphyotrichum ericoides*) and compact stiffstem flax (*Linum rigidum* var. *compactum*) formed a much greater component of the herbaceous vegetation than under redcedar. Some species were completely absent under redcedar cover, e.g. junegrass (*Koeleria pyramidata*).

Most forb and grass species that are common on native prairie in southern Wisconsin were excluded under redcedar through increased shading by the tree. Shade tolerant species such as *Anemone virginiana, Amorpha canescens* and *Physalis virginiana* however, were present under redcedar. The same was true for grasses. Most grass species were excluded from redcedar invaded areas, however the shade tolerant *Panicum oligosanthes* was present. Smooth sumac (*Rhus glabra*) was the only species in this study that was more common under or around redcedar than in native prairie without cedars (McBain 1983). Linneman and Palmer (2006) found that seedlings of woody species were more common under redcedar in encroached grasslands than in prairies without redcedar. A study on the flora of the cedar glades of Tennessee found that herbaceous species occurring in glades dominated by redcedar are more generalist than species occurring in glades without redcedar (Quarterman 1950). In Nebraska, mixed-prairies that were invaded by redcedar retained few of their original flora. Littleseed ricegrass (*Oryzopsis micrantha*) was the only species left. Complete redcedar canopy closure could eventually lead to the full elimination of all native prairie herbaceous species (Kaul and Keeler 1983).

Oneseed juniper (*J. monosperma*) in Arizona has four different influence zones extending from the tree bole outward. In the first zone, which is situated in the direct vicinity of the tree bole, no herbaceous species were found, probably due to shading. In the second zone, which is still underneath the tree canopy, but outside of the direct tree bole area, some herbaceous growth was found, with species typical of mesic conditions

but probably restricted by shading. The third zone, around the canopy and partly shaded by the canopy, represented an area with species typical of xeric conditions, because, as the author argues, this is where the competition for water is greatest. The fourth zone, outside the influence of the tree showed a richer herbaceous community than in the inner three zones (Arnold 1964). In the Oklahoma prairie-forest ecotone, woody species and shade-tolerant species were more common on the northern side of redcedar trees than on more sun-exposed other aspects (Linneman and Palmer 2006).

Similar results have been found for *J. pinchotii* on the Edwards plateau of Texas. Species richness for both graminoids and forbs was lowest directly around the tree bole and underneath the tree canopy. However, at the canopy edge (drip line) and beyond, species richness was higher. This study found the opposite for woody shrubs and succulent species, with most representatives of these two functional groups occurring underneath the juniper canopy and in the direct vicinity of the tree bole (Dye II et al. 1995).

Gehring and Bragg (1992) found differences in herbaceous biomass between areas with and without a cedar canopy that were dependent on species life histories. Shade tolerant species such as *Carex* spp. increase underneath the canopy, whereas shade intolerants such as *Andropogon gerardii, Schizachyrium scoparium* and *Symphyotrichum ericoides* decrease under similar conditions. Jameson (1970b) pointed out that among herbaceous species, forbs declined most in the shady conditions created by redcedar. Older and larger redcedars host little to no herbaceous vegetation below their canopies. However, the vegetation consisted of both C_3 and C_4 species indicating that other ecological or ecophysiological factors than photosynthetic pathway were of importance (Gehring and Bragg 1992).

Eastern redcedar reduces herbaceous biomass underneath its canopy when it invades grasslands. Reductions of biomass were similar under redcedar of different heights (2 m or 6 m) (Engle et al. 1987). In the case of redberry juniper (*J. pinchotii*), the density of forbs and grasses increases with increasing distance from the tree bole. Total biomass increased up to 3 m beyond the canopy influence zone of this juniper species (Dye II et al. 1995).

Sun angle and location under the canopy of juniper influence the herbaceous community. In Oklahoma, herbaceous biomass differed between locations stretching out in four cardinal directions from the tree bole. Northern and eastern sectors generally had lower biomass production due to lower light conditions than those south and west of the main tree stem (Gehring and Bragg 1992).

In one study from a redcedar invaded tall-grass prairie in Nebraska, herbaceous biomass under redcedar was 83% lower than in areas without redcedar cover. Light may have been a driving factor behind this reduction in biomass, because this PPFD decreased in proportion to the increase in redcedar canopy cover. Soil water also decreased under redcedar (11.5%) and it was suggested as a second important factor controlling biomass production (Smith and Stubbendieck 1990). Arnold (1964) suggested that competition for soil water was greatest at the outer fringe of juniper rooting zone where the density of fine roots is greatest. This coincides more or less with the area surrounding the drip line of the tree crown. Closer to the trunk of the tree, light is probably more of a limiting factor. *Juniperus* litter also may be a major factor in the reduction of herbaceous biomass. In conjunction with pinyon pine (*Pinus edulis*), juniper litter caused declines in blue grama (*Bouteloua gracilis*). This was even the case when other factors that could lead to decline of the species, such as shading, root competition or root allelopathic substances were eliminated after multiple regression analysis (Jameson 1966). With no litter influence (one year after removal of redcedar) blue grama increased 23% (Jameson 1970b). Redcedar leaf litter also impacts woody shrub species. Even though a study revealed that seedling density of several woody species declined farther away from the redcedar bole, the higher number of seedlings near the tree showed low rates of emergence compared to those farther away from the tree. This effect was ascribed to deeper litter layers and lower soil temperatures in the direct vicinity of redcedar (Meiners and Gorchov 1998).

Interestingly, herbaceous biomass production under oak cover (*Quercus macrocarpa, Q. ellipsoidalis x velutina*) showed similar patterns as under redcedar. Under cover of oaks, in spite of sufficient soil moisture and nutrients, herbaceous plant biomass is lower than outside of the canopy influence area. Oaks must therefore also slow understory growth due to factors such as lower light conditions or allelopathic

effects. Most of the species that occurred outside the canopy influence area of the oak species involved in the study also occurred inside this area. However, some species were distributed only under oaks while they were not found in open areas surrounding the trees (Ko and Reich 1993).

EFFECTS OF *J. VIRGINIANA* ON WINTERING BIRDS

Similar to the situation for vegetation response, there are more studies examining the effects of redcedar on the ecology of prairie birds than the ecology of forest birds. As redcedar invades the prairie, it produces suitable breeding habitat for many shrubland and woodland birds (Chapman et al. 2004), including uncommon species such as the Loggerhead Shrike (*Lanius ludovicianus*, Tyler 1992, Chabot et al. 2001). However, the patchy habitat created by the invasion of redcedar of the prairies is mostly favored by generalist species such as Eastern Bluebird (*Sialia sialis*) and Cedar Waxwing (*Bombycilla cedrorum*), whereas grassland specialists such as Grasshopper Sparrow (*Ammodramus savannarum*), Cassin's Sparrow (*Aimophila cassinii*), and Western Meadowlark (*Sturnella neglecta*) decline with a higher redcedar incidence (Chapman et al. 2004, Coppedge et al. 2001, Chapman et al. 2004). The conversion of agricultural land to grassland in the Conservation Reserve Program (CRP) benefits many grassland species, even if the restored grasslands consist mainly of non-native grasses. The presence of woody species on CRP land, notably *Juniperus virginiana*, is not tolerated by typical grassland birds (Coppedge et al. 2001, 2006). These specialists show a rapid decline with a redcedar cover of as little as 3% (Chapman et al. 2004). The reasons that these specialists do not tolerate low rates of invasion of *Juniperus virginiana* are not clearly understood, but it is suggested that redcedar cover might be perceived by the birds as habitat for predators or that redcedar obstructs vision (Winter et al. 2000).

There are few studies on the effects of eastern redcedar on breeding bird assemblages in forested areas. There are indications that there is a parallel with native grasslands, because specialized species do not do well in forests with a well developed redcedar midstory. Redcedar has been shown to reduce the availability of suitable breeding habitat for the endangered Black-capped Vireo (*Vireo atricapillus*), which is largely restricted to oak scrub of central Texas (Grzybowski et al. 1994).

Wintering birds have different mechanisms to cope with low temperatures. One of them is the use of sheltered habitats. Coniferous trees are for this reason often preferred over more open deciduous habitats by wintering birds. During cold or rainy weather, birds move from deciduous habitats to coniferous stands, whereas during warm or dry weather, birds are randomly distributed over both types of forest. In a study from southeastern Ohio, this was true for species such as Downy Woodpecker (*Picoides pubescens*), Carolina Chickadee (*Poecile carolinensis*), White-breasted Nuthatch (*Sitta carolinensis),* Brown Creeper (*Certhia americana*), Tufted Titmouse (*Baeolophus bicolor*), and Golden-crowned Kinglet (*Regulus satrapa*) (Petit 1989). In certain cases, coniferous trees do not offer a better protection against the elements than do deciduous trees. In a study from New Jersey a young, uniform stand of eastern redcedar in a field was compared to a mature oak forest with heavy undergrowth and many cavities for winter avian species richness and equitability. The oak forest scored higher for both values than the redcedar stand. Also, in the oak forest, mixed species flocks were more common than in the redcedar stand, where flocks generally consisted of one species. During cold weather some retraction from the redcedar field was observed and this was ascribed to increased exposure to low temperatures relative to the deciduous forest (Kricher 1975). During extremely cold weather, retraction from the entire winter range occurs due to food shortages (Lack 1968) and mortality is higher than usual (Lack 1966).

Birds not only seek to maintain a higher body temperature by staying in coniferous trees, they also use the dense cover to hide from potential predators. A study from Finland showed that Willow (*Poecile montanus*) and Crested Tits (*Lophophanes cristatus*) preferred the densest, interior parts of coniferous trees when predation risk was high. This occurred in winters when voles (*Microtus* spp.), an important prey item of Eurasian Pygmy-Owl (*Glaucidium passerinum*), were scarce, and the owls preyed solely on parids (Suhonen 1993).

Conelets of the genus *Juniperus*, which resemble berries because of their fleshiness, are a good source of food for many animal species. Mammals such as Raccoons (*Procyon lotor*) and Gray Fox (*Urocyon cinereoargentus*) readily eat redcedar conelets. However, the bulk of the consumption of redcedar conelets occurs by birds. About 60% of redcedar conelets are eaten by birds in open areas, whereas in forested

areas, this number can be 90-100% (Phillips 1910). Seeds in plant species that do not produce a fruit or berry are mostly digested by birds and having passed through the digestive tract, no longer germinate (McAtee 1947). However, in the case of redcedar, which does produce a protective conelet around the seed, seeds pass the digestive tract unharmed (Phillips, 1910). Redcedar is often found growing along fence lines (Phillips 1910, McAtee 1947, Holthuijzen and Sharik 1984) because birds that consume redcedar conelets leave droppings when the perch on the fence. The species is also frequently found under tall trees, due to the preference of birds to roost in tall trees. This, in combination with the fact that forest soils are more stable than grassland soils, causes redcedar seeds to germinate easily after being dropped by birds (Phillips 1910).

Fruits and berries form an especially important food source for birds during migration and winter, due to the fact that protein-rich insects are mostly absent during this time in temperate climates (Parrish 2000). Redcedar conelets are available from early fall through late spring. They have a purple color, and fruits have a whitish bloom, which increases visibility to birds. Moreover, conelets remain available even with heavy snowfall, when most seeds from herbaceous plants and seeds that have fallen on the ground are invisible. Conelets are also relatively large proportional to other seeds and berries (0.4–0.6cm) which increases visibility further. The protein content of redcedar conelets is 4–6%, sugar content is 10–30% and starch/cellulose content is 12–20%. In addition to this, conelets also contain nutritious volatile oils, acids, and minerals (Phillips 1910). For birds, which have high metabolic rates compared to mammals, it is important to take in large amounts of energy-rich foods. Bohemian Waxwings (*Bombycilla garrulus*) have been found to ingest over 900 conelets of *J. scopulorum* in five hours (Phillips 1910). A study from Rhode Island showed that there were generally two types of seeds, those that were high in energy (with plenty of carbohydrates and fats) and those with high levels of protein. Intake of large amounts of one type usually had to be supplemented by ingestion of smaller amounts of the other type, to satisfy both the high energy demands of fast metabolism in birds and longer term essential nutritional demands. Redcedar conelets combine high energy content with high levels of protein and are therefore often preferred food by birds (Smith et al. 2007). Phillips (1910, p. 13) concludes that ‘the lines of bird migration and numbers of birds, prevalence of juniper

berries and scarcity of other bird food are undoubtedly factors which affect the distribution of the juniper.'. Phillips also provides a short list of species that have been found consuming redcedar conelets. Central Oklahoma wintering birds included in this list are:

-Downy Woodpecker (*Picoides pubsecens*)
-Yellow-bellied Sapsucker (*Sphyrapicus varius*)
-Northern Flicker (*Colaptes auratus*)
-Cedar Waxwing (*Bombycilla cedrorum*)
-American Crow (*Corvus brachyrhynchos*)
-Northern Mockingbird (*Mimus polyglottos*)
-Hermit Thrush (*Catharus guttatus*)
-Eastern Bluebird (*Sialia sialis*)
-Yellow-rumped Warbler (*Dendroica coronata*)
-Fox Sparrow (*Passerella iliaca*)
-Purple Finch (*Carpodacus purpureus*)

Protein-rich insects are often an important addition to avian diets to compensate for the intake of seeds low in proteins (Smith et al. 2007). In summer, insects are abundant in northern hemisphere temperate climates, but in winter this is not the case. However, insectivorous birds are often still able to find sufficient food during this time in temperate areas, especially in southern areas within the northern hemisphere such as the southwestern U.S (Morse 1970, Austin and Smith 1972) where insects are active during the winter in areas with increased shelter and a warm microclimate. Evergreen trees with a high LAI, such as conifers, form an especially important winter habitat for insects (Danks 1991). In Sweden, *Picea abies* is host to at least 19 arachnids and several insect species during winter. The insects and spiders form a substantial part of the diet of small passerines such as Goldcrest (*Regulus regulus*), three species of tit (*Paridae*) and Eurasian Treecreeper (*Certhia familiaris*). These species all have their ecological equivalents in North America (Ruby-crowned Kinglet (*Regulus calendula*), chickadees and titmice (*Poecile* spp. and *Baeolophus* spp.), and American Creeper (*Certhia americana*). No preference for a particular species of insect or arachnid was shown.

Nutritional value of spiders declined with the progression of winter months (Norberg 1978).

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CHAPTER III

CHANGES IN FOREST UNDERSTORY ASSOCIATED WITH *JUNIPERUS* ENCROACHMENT IN OKLAHOMA, U.S.A.: THE IMPORTANCE OF LEAF LITTER

ABSTRACT

I studied changes in understory vegetation due to encroachment of *Juniperus virginiana* resulting from anthropogenic fire suppression into the midstory of Cross Timbers forests dominated by *Quercus* spp. in Payne County, north-central Oklahoma, U.S.A. I hypothesized that the *J. virginiana* alters its physical environment such that plant species composition change and vegetation cover and richness decline along a gradient as the influence of the *J. virginiana* midstory increases. I compared vegetation in forest gaps, forests without *J. virginiana*, at the inner and outer edge of *J. virginiana* and near trunks (200 plots total). Species richness (11 to 6 spp. m^{-2}) and cover (53.3 to 12.7%) declined with proximity to *J. virginiana* trunks. Regression analysis indicated that richness (R^2=0.08) and cover (R^2=0.18) were best explained by *J. virginiana* litter mass. Partial canonical correspondence analysis (pCCA) revealed two strong canonical axes, one related to litter/light and the other to cover of *Quercus* spp. versus *J. virginiana*. Tree seedlings and woody vines dominated near *J. virginiana* trunks. Forbs, graminoids and *Quercus* spp. seedlings were more common in areas without *J. virginiana*. My study indicates that litter is the main determinant of understory vegetation declines associated with midstory juniper encroachment in these fire-suppressed forests. Decreases in herbaceous litter loads, which historically contributed to the accumulation of fuel beds, will have a positive feedback effect for further midstory encroachment. Declines in recruitment of *Quercus* spp. that were related to increasing abundance of *J. virginiana* and consequent increases in litter loads may lead to changes in overstory composition.

KEYWORDS: Midstory development, Juniperus virginiana, Herbaceous vegetation, Oklahoma, PPFD

INTRODUCTION

Anthropogenic fire exclusion can have a profound effect on forest structure and density. Fire-sensitive woody species encroach with fire suppression and often form a dense midstory (Waldrop & Lloyd 1991; Glitzenstein et al. 1995; Grice 1997; Blankenship & Arthur 2006). Fire suppression in North America has led to marked increases of *Juniperus* spp. (Cupressaceae), notably *J. virginiana* L. (Bragg & Hulbert 1976; Briggs et al. 2002; Sheley & Bates 2008). While most *Juniperus* spp. of the North American West and Southwest are encroaching in semiarid, and open landscapes, *J. virginiana* is a widespread eastern species that is spreading in prairies but also in forests throughout the Great Plains (Bidwell et al. 2000).

In many cases, the overall structure of fire-suppressed forests is characterized by high stem density, relative young stand age and high litter accumulation (Covington & Moore 1994; Kaufmann et al. 2003; Rogers et al. 2007; Vanhaa-Majamaa et al. 2007). These features can reduce understory light conditions which negatively affects shade-intolerant understory species (Thomas et al. 1999; Pagès et al. 2003). Moreover, the buildup of a deep litter layer can alter the chemical, physical and hydrological environment in the soil which often results in lower understory recruitment (Anderson et al. 1969; Facelli & Pickett 1991). There are several documented examples of understory decline related to fire suppression from the southeastern United States where *Quercus* spp. and other hardwoods cause understory vegetation to decline in *Pinus taeda* L. and *P. palustris* Mill. ecosystems (Blair & Feduccia 1977; Provencher et al. 2001a; Hiers et al. 2007). Similar reductions in understory vegetation caused by the development of midstories of encroaching woody species through land use changes such as increased urbanization and associated fire frequency changes and alterations in climate (atmospheric CO_2 increases) are observed in other parts of the world, such as in riparian forests in the southern United States (Ostrom & Loewenstein 2006) or in systems dominated by *Eucalyptus camaldulensis* Dehnh. in southern Australia (Price & Morgan 2008).

With fire suppression in the Cross Timbers forest of central Oklahoma, *J. virginiana* often forms dense midstories under a canopy of broadleaved trees including two dominant *Quercus* species, *Q. stellata* Wangenh. and *Q. marilandica*

Münchh. (Engle & Stritzke 1995) and drastically alters the open character of the forest. Understanding how *J. virginiana* alters the understory environmental conditions in Cross Timbers forests may have important implications for understory plant diversity and productivity. In prairies, *J. virginiana* encroachment has the potential to increase litter depth (Norris et al. 2001a), raise soil pH through litter depositions (McBain 1983), decrease soil carbon stores (Norris et al. 2001a) and lower understory light conditions (Linneman & Palmer 2006).

While there may be some similarities in the response of understory vegetation in prairies and the Cross Timbers forest, there are several distinctions. The structure of the forest ecosystem differs from prairies through the presence of an arboreal overstory layer. The combination of an overstory of *Quercus* spp. and a midstory layer of *J. virginiana* may exacerbate environmental conditions such as light environment, understory temperature and precipitation throughfall relative to prairies invaded by *J. virginiana*. *J. virginiana* in forests is subject to competition with overstory trees, which may lead to differences in stem growth, crown depth and foliar biomass compared to mature *J. virginiana* in prairies, which mainly compete with grassland species for belowground resources. Additionally, understory communities in native grasslands are compositionally different from understory communities in forest ecosystems. Though they share some species, North American prairies are generally dominated by C_4 grass species that are physically adapted to warm, high light growing conditions, while forest understories tend to be dominated by C_3 shade-tolerant forbs and woody species.

Understanding the changes in understory productivity, richness, and composition relative to an increase in *J. virginiana* midstory is important, as these changes have the potential to alter biodiversity and dynamics of the vegetation in Cross Timbers forests and alter habitat for taxa other than vascular plants. Cross Timbers forests generally have an open character. Lack of disturbance can lead to canopy closure which lessens the vulnerability to fire due to reduced production of fine fuels (Johnson & Risser 1975). The development of a midstory of *J. virginiana* may further alter the production of fine fuels and regeneration of the dominant *Quercus* species leading to the 'mesophication' (Nowacki & Abrams 2008) of this otherwise open, fire-dependent ecosystem. Understanding the effects of *J. virginiana* encroachment in the Cross Timbers is directly applicable to a large area (~79,000 km²; Kuchler 1964) of similar fire suppressed forest in Oklahoma, Kansas, and Texas.

On a broader scale, this understanding provides general insight into the effects of midstory development caused by anthropogenic fire suppression on forest understory vegetation.

The objectives of this study were to determine the effects of *J. virginiana* encroachment on the understory physical environment and plant communities of *Quercus*-dominated Cross Timbers forests of Oklahoma. I hypothesized that understory species richness and cover decrease with increasing *J. virginiana* encroachment. Furthermore, I hypothesized that changes in understory composition will be more pronounced closer to redcedar trunks. Of the changes in the physical environment related to *J. virginiana* encroachment, I predicted that leaf litter accumulation is the major factor related to changes in understory vegetation.

METHODS

Study sites

During 2008, I conducted research at ten 1 ha sites approximately 15 km west of Stillwater, Oklahoma. Five sites were located around Lake Carl Blackwell (LCB) (36.12˚, -97.21˚) and five were on and around the Oklahoma State University Cross Timbers Experimental Range (CTER) (36.04˚, -97.21˚). The research area is located at the western edge of the Cross Timbers forest which forms a transition zone between the tallgrass prairie and eastern North American forests. The sites were dominated by *Quercus stellata*, *Q. marilandica* and *Sideroxylon lanuginosum* Michx. All sites were characterized by a variable *J. virginiana* component in the midstory. Additional frequent tree species included *Quercus muehlenbergii* Engelm., *Celtis occidentalis* L., *C. laevigata* Willd. and *Ulmus americana* L. Soils were predominantly Stephenville-Darnell-Niotaze associations that are ustalfs of a fine, sandy loam texture (USDA, NRCS 2008c). Three sites near LCB and two at CTER were burned three to ten years before the study. It was not possible to determine the spatial pattern of previous fires or fire intensity within sites in relation to individual plots. However, to minimize potential effects of recent fire history on environmental conditions in my research plots, I selected sites where burns had no lasting visual effects on canopy cover of *J. virginiana* or other tree species.

Sampling design

At every site, I included four blocks of five different environmental conditions or 'categories' in 1 m² plots (20 plots at each site, 200 plots total). The first category (open) consisted of a forest gap, with minimal light interception from *Quercus* or *J. virginiana* canopies and a negligible amount of tree leaf litter. The remaining four categories were located under an overstory of *Quercus* spp. with varying levels of *J. virginiana* influence. The second category (oak) consisted of closed-canopy forest of *Quercus* spp. with litter of *Quercus* spp. and canopy light interception by *Quercus* spp. only. The third category (outer edge) extended outward from the edge of *J. virginiana* drip line such that *J. virginiana* contributed little to the litter layer and had some influence on light interception. The fourth category (inner edge) consisted of the area from the *J. virginiana* drip line inwards towards the trunk of the tree such that *J. virginiana* had both an influence on litter and light interception. The fifth category (trunk) abutted the trunk of *J. virginiana* trees such that light levels were reduced and *J. virginiana* leaf material was the major litter layer component.

I sampled understory vegetation during early May and again in mid-August to account for both spring ephemerals and cool-season as well as warm-season species. I determined the relative cover of all vascular plants within the 1 m^2 plots using ocular estimation and a Daubenmire scale modified to the midpoint of the cover range (Towne et al. 2005). I identified all herbaceous species, as well as seedlings and saplings of all woody species less than 1.37 m tall. I assessed total understory cover during the spring and summer vegetation sampling periods using regular digital photographs taken from above the maximum height of understory vegetation (1.37 m). I quantified canopy openness, direct photosynthetic photon flux density (PPFD) and diffuse PPFD directly above the top of understory vegetation for each plot using a digital camera with a hemispherical lens. I took all pictures on overcast days during early July to reduce sunshine glare. I used WinScanopy and XlScanopy software (Régent Instruments 2006) for analysis of regular and hemispherical photographs. I determined which trees around each plot influenced light interception and litter inputs using a Basal Area Factor 10 (BAF; number of units of cross sectional area represented by each tree stem) angle gauge. In addition to basal area of each species, I recorded Diameter at Breast Height (DBH; diameter measured at 1.37 m) of sampled trees with calipers (±0.1 cm) to estimate overstory size class distribution.

Leaf litter type and quantity were measured in June/July in two areas adjacent to each plot (0.04 m^2). After collection, I separated litter into the categories deciduous tree (primarily of *Quercus* spp.), *J. virginiana* and herbaceous. Litter of each category was then dried to constant weight (60^oC) and weighed to the nearest gram. At the same time, I collected and bulked soil samples (0 - 15 cm depth) from two opposite corners of each plot. The Oklahoma State University Soil, Water and Forage Analytical Lab then performed analyses for NH_4 and NO_3 concentration using 1 M KCl extraction on a latchet flow-injection analyzer. For determining NO_3 concentration, cadmium reduction was used and for NH_4 concentration the salicylate procedure. I determined soil pH for each sample using 1:1 soil-H_2O solutions (USDA, 2008b) and a scientific pH meter (Thermo Fisher Scientific, Waltham, Massachusetts) (±0.01 pH).

On July 27th and 28th, which were characterized by the absence of cloud cover and wind < 5 $km.h^{-1}$, I measured soil temperature, air temperature and relative humidity at each plot. I measured soil temperature using a probe thermometer (±1°C) and air temperature (±0.1°C) and relative humidity (±0.1%) above the understory vegetation level using a Kestrel 3000 weather meter (Nielsen-Kellerman Inc., Boothwyn, Pennsylvania). I sampled volumetric soil moisture (0-20 cm depth) on August 30th and September 1st (both days were at least 48 hours since the last rainfall) using a Mini Trase soil moisture system (±0.1%) with time-domain reflectometry technology (Soilmoisture Equipment Corp., Santa Barbara, California).

Statistical analyses

I performed ANOVA and Duncan's *post hoc* multiple comparison (SAS 9.1 statistical software package; SAS Institute Inc., 2003) to test for differences in environmental variables as well as in understory vegetation richness and cover among categories of varying *J. virginiana* influence. Before conducting ANOVA, I tested variables for normality and heteroscedasticity and transformed the data using logarithmic or arc-sine transformations as needed. I used a series of simple regressions (α=0.05) to determine which environmental variables were related to summer understory cover and total species richness (total species richness was calculated as the total number of species found in a plot during both the spring and summer sampling periods). I chose summer understory cover and total species richness because these variables

represented a more complete sample of understory plant productivity and overall species richness than spring vegetation variables. I determined covariance among variables included in the regression analysis. Results for regressions including and excluding the 'open' plots yielded similar relationships. Therefore, I present data from tests excluding the 'open' plots to focus on changes and processes within the Cross Timbers forest. I performed partial canonical correspondence analysis (pCCA, Ter Braak 1986) on my species data to determine compositional structure among plots. I used categories (excluding 'open') as nominal variables. To determine the relationships between the environmental variables and my categories and to establish correlational structure between the environmental variables I included environmental variables as (passive) supplemental variables. I performed partial analysis because it included my sites (defined as blocks) as covariables. I included only species that occurred more than 10 times (5% occurrence), because the growing conditions in plots where species were found that were rare in my study may not have been typical for these species given their small sample size. I used CANOCO for Windows 4.5 (Ter Braak & Šmilauer 2002) for all ordination analyses.

RESULTS

Stand characteristics

Across all ten sites, total basal area of trees ranged from 8.9 to 28.0 $m^2.ha^{-1}$. *Q. stellata* contributed on average 54.5% to total BA; *J. virginiana* 26.9%; *Q. marilandica* 10.3%, and other hardwoods 8.3%. Sites also varied in regards to average tree DBH ranging between 16.6 and 25.8 cm. However, when compared across categories, mean BA and DBH showed minimal variation (Table 1). *Q. stellata* had the greatest mean DBH (24 cm), followed by *J. virginiana* (22 cm) and *Q. marilandica* (18 cm). Canopy openness ranged from 22.5% to 31.1% between sites and did not significantly vary among the four categories with forest cover. Mean canopy openness across all plots was 25.7%.

Environmental variation between categories

Micrometeorological variables showed a consistent pattern with increasing *J. virginiana* (category effect $P<0.01$; Table 1). Air temperature was highest in the open plots and declined somewhat towards the *J. virginiana* trunk. The difference in mean

temperature between open and trunk plots was 1.9°C. Relative humidity increased by 1.5% from open plots to plots close to *J. virginiana* trunks. Similar to air temperature, soil temperature decreased 4°C from the open to the trunk plots. Volumetric soil moisture decreased 2.2% with increasing distance from the *J. virginiana* trunk.

Total PPFD (Fig. 1) was greatest in the open plots, intermediate in oak plots and at the outer edge of *J. virginiana*, and lowest at the inner edge of *J. virginiana* and near the trunk (category effect $P<0.01$). Because direct PPFD contributed 85.9% of total PPFD, the pattern of direct PPFD change among categories was similar to total PPFD. Diffuse PPFD levels in the forested categories were lower than the open category. The pattern of diffuse PPFD among categories was similar to direct and total PPFD.

Total nitrogen concentration in soils of all forest categories was similar and higher than 'open' categories. Ammonium (Table 1) composed the majority of total nitrogen and had a pattern among categories similar to total nitrogen. Nitrate concentration in the open plots was lower than the oak and trunk plots. Soil pH increased under *J. virginiana* with values of the trunk plots greater than plots not under *J. virginiana* canopies (Table 1).

Total litter mass generally increased from the open to the trunk categories, with the exception of the outer edge category (Fig. 1). Grass litter was highest in open plots but negligible in forest plots. Hardwood litter was greatest in the oak plots and *J. virginiana* litter increased with proximity to *J. virginiana* trunks. On average, total litter comprised 57.3% *J. virginiana* litter, 38.5% hardwood litter, and 4.2% herbaceous litter.

Species richness and vegetation cover

Understory plant species richness for both spring and summer sampling periods decreased along the gradient towards the trunk of *J. virginiana*. Mean spring species richness decreased from 8.0 m^{-2} to 4.6 m^{-2} and mean summer species richness decreased from 7.3 m^{-2} to 3.7 m^{-2} between the open and trunk categories, respectively. When spring and summer measurements were combined, total species richness decreased from 10.8 m^{-2} to 5.8 m^{-2} along the same gradient (Fig. 2). While mean total richness was greatest in the open plots (Fig. 2), maximum species richness for an individual plot was 17 m^{-2} and measured in an oak plot. Total vegetation cover in both

spring and summer increased about fourfold between the trunk plots and open plots (Fig. 2).

Environmental variables related to vegetation changes

Regression revealed significant (α=0.05) correlations between total richness and *J. virginiana* litter mass, grass litter mass and diffuse PPFD (Fig. 5). For summer vegetation cover, there were significant correlations with *J. virginiana* litter mass, total litter mass, and direct PPFD. *J. virginiana* litter mass predicted the largest amount of variation in both summer cover and total richness. While relationships with PPFD and grass litter were statistically significant, these variables had little explanatory value. There was little covariance among the independent variables representing litter and light; *J. virginiana* litter and diffuse PPFD (r=-0.083, *P*=0.297), grass litter and diffuse PPFD (r=0.020, *P*=0.800), direct PPFD and *J. virginiana* litter (r=-0.112, *P*=0.160), and direct PPFD and total litter (r=0.147, *P*=0.064). *J. virginiana* litter and grass litter had minimal covariance (r=-0.149, *P*=0.060). Total litter and *J. virginiana* litter covaried (r=0.662, *P*<0.001), which is expected since *J. virginiana* litter comprises 85.9 % of total litter. This covariance indicates that the relationship between summer vegetation cover and total litter was largely a function of the *J. virginiana* component. Given fairly low R^2 values, a large portion of variation remained unexplained. When variation among sites was included in an analysis of covariance, R^2 values increased substantially. For instance, when site variation was included in the model, *J. virginiana* litter explained 40.9% of variation in total species richness and 44.9% of the variation in summer vegetation cover.

Species composition

I found that open plots were dominated by species mostly absent in the four forest categories. Also, herbaceous vegetation cover was consistently much higher in open plots. These results are expected given the large environmental differences between forest gaps and forest understory. Since my objectives related to understanding changes in understory composition with *J. virginiana* encroachment within the forest, I restricted my analysis of vegetation changes to the forest plots (omitted the open plots).

Partial canonical correspondence analysis (pCCA), including sites as blocks, identified two strong canonical axes (Fig. 6a). The first axis indicated a gradient of (*J. virginiana*) influence, with decreasing light and increasing litter. The second axis explained less than half of variability in species composition relative to the first axis and was related to the effects of *Quercus* spp. versus *J. virginiana* on the understory plant community. When this division in my pCCA with the environmental variables was plotted against the categories (Fig. 6b), the majority of the second axis explained variability related to *Quercus* spp. litter effects or direct PPFD.

Species were mostly found in the central area of the pCCA diagram, away from the categorical centroids. This area lies between the inner edge/outer edge and oak categories, confirming that most species are generalists, without a distinct preference for environmental differences in any of the categories. However, conditions found directly around the *J. virginiana* trunk were unfavorable for herbaceous vegetation given the distance between the trunk centroid and the species points. There was, however, a number of species that were centered at the inner edge or tended to occur most in areas close to the trunk. These include the vines *Smilax bona-nox* L., *Vitis rotundifolia* Michx. and *Parthenocissus quinquefolia* (L.) Planch. Only a small number of forbs such as *Galium circaezans* Michx., *Parietaria pensylvanica* Muhl ex Willd. and *Myosotis verna* Nutt. occurred fairly frequently in areas relatively close to *J. virginiana*. However, a number of tree species were well represented in the area between the *J. virginiana* trunk and the inner edge, including seedlings of *Ulmus americana, U. rubra, Celtis occidentalis, C. laevigata,* and *Sideroxylon lanuginosum. J. virginiana* seedlings also were associated with *J. virginiana* adults. In contrast, seedlings and saplings of *Quercus stellata, Q. marilandica* and especially *Q. muehlenbergii*, were mostly centered closer to the oak centroid. The clonal shrub *Symphoricarpos orbiculatus* Moench. was best represented closer to oak centroid, as were a small number of forest forbs including *Geum canadense* Jacq. and *Sanicula canadensis* L. Some species typical of grasslands such as *Schizachyrium scoparium* (Michx.) Nash., *Elymus canadensis* L. and *Dichanthelium oligosanthes* Gould were centered in the area between the outer edge of *J. virginiana* and in oak plots. Species that were represented in areas with higher PPFD in my study include two sedges and three species of grass, including C_3 species such as *Dichanthelium oligosanthes* and *Elymus canadensis.* In addition, the forb *Gamochaeta purpurea* (L.) Cabrera and the legume *Lespedeza virginica* (L.) Britton

were concentrated in this area; both species are more typical of open conditions. Frequencies of understory species in the four categories (Table 2) revealed similar results to the pCCA analysis, with tree seedlings and vines generally common in trunk categories, and *Quercus* spp., forbs and grasses more common in oak and outer edge categories. All species found under *J. virginiana* were also observed in oak plots, where they were often more common.

Environmental variables

Environmental variables were passively included in the pCCA. This illustrated how environmental variables were distributed over the four forest categories (Fig. 4b) and it revealed that *J. virginiana* litter comprised an important part of total litter mass. *J. virginiana* litter was also the strongest environmental factor in the diagram. Furthermore, total litter mass and litter cover were strongly related given their proximity and shared direction in the diagram. Light variables tended to be higher in oak plots and at the outer edge of *J. virginiana*. Diffuse PPFD was the strongest light related factor. Variables related to soil nitrogen and soil pH showed no specific relationship with any category.

DISCUSSION

Declines in vegetation cover and species richness that were related to increasing proximity to *Juniperus virginiana* trunks were mainly associated with changes in litter dynamics and, to a lesser extent, changes in light environment. In as much as litter and light variables did not covary, the stronger relationship with litter than light indicates that *J. virginiana* litter was probably the most important factor explaining understory changes in response to the development of a *J. virginiana* midstory. Similar evidence was found by other studies on midstory encroachment (Provencher et al. 2001a; Wearne and Morgan 2004; Hiers et al. 2007; Price and Morgan 2008). The accumulation of leaf litter can have a detrimental effect on plants through a variety of mechanisms including the formation of a mechanical barrier that inhibits germination, alterations in the chemical environment of the upper soil layer and reductions of light available to germinating seeds (Sydes & Grime 1981; Facelli & Pickett 1991). Based on my data, growing conditions were particularly unfavorable to understory plants close to the trunk and below the inner edge. There were similar

declines in species richness and cover with increasing proximity to *J. virginiana* trunks in prairies encroached by the *J. virginiana* (McBain 1983; Engle et al. 1987; Linneman & Palmer 2006).

J. virginiana had a greater effect on plant cover than on species richness in prairie ecosystems (Linneman & Palmer 2006), as in my study. Likewise, in previous studies of forest systems, vegetation cover declined to a greater extent than species richness concurrent with litter accumulation associated with fire suppression (Provencher et al. 2001b; Hiers et al. 2007). One reason for greater sensitivity of cover than richness with increasing litter could be related to the persistence of seed under litter layers (Wearne and Morgan 2006). The effects of dense *J. virginiana* canopies on seed dispersal are unknown. Seed collisions with *J. virginiana* foliage may unequally distribute the seed rain, contributing to declines in understory richness and density under *J. virginiana*. Alternatively, *J. virginiana* might act as seed traps, similar to other woody plants such as shrubby Ericaceae spp. (Bullock & Moy 2003).

Decreasing richness with increasing proximity to *J. virginiana* is intuitive and evident from my study. However, the use of small-scale plots such as in my study may not completely capture species richness differences among categories due to the rarefaction effect (Palmer et al. 2000). This effect describes the inherent link between vegetation density and species richness. Since herbaceous cover is consistently low near *J. virginiana*, species richness data in this habitat may not be complete. The appearance of herbaceous litter as a significant variable in predicting richness may also be an artifact of the rarefaction effect because the amount of litter may have an incidental linkage with species richness.

My findings of lower temperature, higher relative humidity and lower soil temperature under *J. virginiana* in forest systems are expected due to increased shading and litter accumulation and consistent with studies focusing on *J. virginiana* in prairies (Norris *et al.* 2001; Smith & Johnson 2003; Linneman & Palmer 2006; McKinley 2006; McKinley *et al.* 2008, Pierce & Reich 2009). Absolute differences in relative air humidity and temperature among habitat categories were small and inconsistent with changes in herbaceous cover and species richness leading us to speculate that differences in temperatures and relative humidity among categories play a relatively minor role in determining plant richness and productivity.

Later successional species, including many tree species, usually have larger seed size and greater energy stores. Several authors argue that this is a characteristic

that permits these species to penetrate dense litter mats during germination and establishment (Grime 1979; Tao et al. 1987). However, *Quercus* spp., which have the largest seeds in this study, were not well represented under or near *J. virginiana*. Given the even distribution of the *Quercus* spp. overstory throughout my study areas, this was somewhat unexpected. The avoidance of *Quercus* spp. in areas dominated by a *J. virginiana* midstory may relate to soil pH. The maximum tolerable soil pH for *Q. marilandica* is 5.6 (USDA, NRCS 2008a). In my study, I found soils near *J. virginiana* trunks less acidic (above 6.0) than soils farther away from trunks. Previous studies also found that the *J. virginiana* increases soil pH (Coile 1933; Spurr 1940; Read & Walker 1950; McBain 1983) and ascribed the increase to the high calcium content of *J. virginiana* leaves and litter. Recent declines of *Q. marilandica* recruitment in the region (Bruner 1931; Johnson & Risser 1975; Hoagland *et al*. 1999) may in part be related to increases in soil pH associated with the development of a *J. virginiana* midstory. Soil pH preferences for *Q. stellata* (pH 4.8-7.0, USDA, NRCS 2008a) and *Q. muehlenbergii* (pH 6.5-7.0+, Limstrom 1965) have a wider range than those for *Q. marilandica.* If indeed *J. virginiana* has a negative effect on *Quercus* spp. recruitment, the increasing abundance of the species will not only affect the understory, but eventually may affect the forest overstory.

The presence of vines in the understory beneath *J. virginiana* may be explained by their ability to survive in low light environments. Vines which use tendrils to climb, including *Parthenocissus quinquefolia*, *Smilax* spp. and *Vitis* spp. are well adapted to grow in environments with low PPFD (Carter & Teramura 1988). The presence of vine species under the *J. virginiana* may however also be explained by their tolerance to thick litter layers. The vines in my study are characterized by large seeds, which may increase germination success (Facelli & Pickett 1991). The few species of forbs that I found in dense *J. virginiana* areas are all species that grow and flower early in the spring when light levels in the understory are higher because the canopies of overstory trees have not yet fully developed. Even though they are shade tolerant (Weaver 1954; Buss 1956; USDA, NRCS 2008a), the grasses *Dichanthelium oligosanthes* and *Elymus canadensis*, both declined with increasing proximity to *J. virginiana*. Many grass species found in the study areas and adjacent prairies (e.g. *Andropogon gerardii*, *Chasmanthium latifolium*, *Schizachyrium scoparium*) reproduce asexually. As such, the species may be able to persist under *J. virginiana*, regardless of the potential effects on seed germination. However,

conditions of increased litter and lower light probably decrease crown sizes and cover of these grasses which may contribute to the greater decline in understory cover than species richness with proximity to *J. virginiana.* In southern Wisconsin, *Dichanthelium oligosanthes* was the only grass species under *J. virginiana* in prairies (McBain 1983). McBain observed that other grasses were not present around the species, even after removal of the trees and suggested allelopathic effects of littter as a possible explanation. Likewise, I propose that the decline of shade-tolerant graminoids close to *J. virginiana* was related to litter rather than light availability.

J. virginiana has tolerance for a wide range of pH, soil moisture, light levels and other environmental factors (Lawson & Law 1983; Eggemeyer et al. 2006). I found *J. virginiana* seedlings in all habitat categories, but most commonly under mature conspecifics. This finding is consistent with another study on the closely related *J. ashei* (Van Auken et al. 2004) that found seedlings occurred in all habitats within a *Juniperus* woodland. However, *J. ashei* seedlings were most common in direct vicinity of mature *J. ashei* trees (Jackson & Van Auken 1997; Van Auken et al. 2004) due to a combination of dispersal constraints and higher mortality farther away from the parent tree.

A well-developed *J. virginiana* midstory will make the forest more resistant to surface fires, more susceptible to crown fires, and decrease the ability to implement prescribed burning. Increasing *J. virginiana* abundance in the midstory of Cross Timbers forests is related to decreasing fire frequency because the species is not able to survive fires that cause crown scorch and does not sprout following topkill (Engle & Stritzke 1995). On the contrary, *Quercus stellata* is a fire-tolerant species and is the natural dominant species in the Cross Timbers which historically had a fire return interval of approximately 10 years (Abrams 1992; Guyette et al. 2002). Overall, fire suppression has led to increases in fire-sensitive, shade-tolerant species throughout the eastern United States, at the expense of fire-tolerant heliophytes. This process of forest 'mesophication' (Nowacki and Abrams 2008) is illustrated by the increasing presence of *J. virginiana* biomass and related declines in herbaceous biomass. Reductions in understory productivity further facilitate *J. virginiana* encroachment because fine fuel accumulation is a direct function of understory productivity. As *J. virginiana* is largely immune from surface fire once it reaches 2 m in height (Bidwell et al. 2002), the accumulation of a *J. virginiana* midstory becomes permanent unless a crown fire occurs, which has a high risk to people and property. Crown fires are

historically uncommon in the Cross Timbers but are becoming more common due to the inclusion of the highly flammable *J. virginiana* (Bidwell et al. 2000). Therefore, to maintain the ecological integrity of the Cross Timbers forest and maintain forests that are resistant to catastrophic crown fires, prescribed burning should be implemented to reduce *J. virginiana* encroachment. Once *J. virginiana* encroachment reaches a point where herbaceous biomass (fine fuels) declines, more expensive mechanical treatments are necessary.

The long term community- and ecosystem-level effects of midstory development in otherwise more open forest ecosystems are largely unknown. My study and several others indicate a decline of forest understory communities with midstory encroachment and indicate that litter is the most likely candidate for explaining variation in understory vegetation (Provencher et al. 2001a; Hiers et al. 2007). In the Cross Timbers, the development of a midstory through encroachment resulting from anthropogenic fire suppression not only affects the herbaceous community but also the regeneration and future composition of the overstory community and has consequences for ecosystem function and resilience to disturbance. The increasing human influence on pyric frequency can have strong effects on forest structure and biodiversity in fire-dependent forested ecosystems wherever there is a potential for the release of fire-sensitive woody species.

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Table 1: Means (±1 S.E.) of stand structure, canopy, micrometeorological and soil variables.

Category	Total BA (m^2ha^{-1})	Mean diameter (cm)	Openness (%)	Temp. air (°C)	Relative humidity (%)	Temp. soil (°C)	Vol. soil moisture (%)
Open	0 b	0 B	50.3 ± 1.9 a	35.7 ± 0.2 a	54.0 ± 0.9 b	23.1 ± 0.1 a	11.4 ± 1.0 a
Oak	14.3 ± 0.1 a	20.3 ± 3.2 A	18.6 ± 0.7 b	34.0 ± 0.2 bc	54.7 ± 0.8 ab	20.8 ± 0.1 b	10.1 ± 0.7 bc
Outer edge	15.2 ± 0.1 a	22.5 ± 3.6 A	21.0 ± 1.0 b	34.3 ± 0.2 b	53.6 ± 0.9 b	20.8 ± 0.1 b	10.0 ± 0.7 bc
Inner edge	15.6 ± 0.1 a	21.0 ± 3.3 a	19.4 ± 0.7 b	34.0 ± 0.2 bc	54.6 ± 0.8 ab	20.2 ± 0.1 c	10.3 ± 0.8 b
Trunk	15.7 ± 0.1 a	22.9 ± 3.6 a	18.9 ± 0.7 b	33.7 ± 0.2 c	55.5 ± 0.7 a	19.3 ± 0.1 d	9.2 ± 0.5 c

Total basal area is the cross sectional area of trees at 1.37 m. Mean diameter is the mean diameter of trees measured at 1.37 m. Openness is the percent of sky not obscured by canopies. Lower case letters indicate significant difference among categories (Duncan's *post hoc*, α=0.05).

Table 2: Species found in the four forest treatments with their frequencies (% of plots).

Species code	Scientific name	Growth form[a]	Frequency				
			Oak	Outer Edge	Inner Edge	Trunk	All
AMPS	*Ambrosia psilostachya*	F	15	15	12.5	7.5	12.5
CABU	*Carex bushii*	G	17.5	20	15	10	15.6
CAOL	*Carex oligocarpa*	G	17.5	17.5	15	7.5	14.4
CECA	*Cercis canadensis*	T	5	7.5	7.5	17.5	9.4
CELA	*Celtis laevigatus*	T	7.5	2.5	7.5	15	8.1
CEOC	*Celtis occidentalis*	T	55	55	37.5	50	49.4
CODR	*Cornus drummondii*	S	7.5	2.5	17.5	7.5	8.8
DIOL	*Dichanthelium oligosanthes*	G	30	32.5	15	10	24.4
ELCA	*Elymus canadensis*	G	20	25	15	10	17.5
ERST	*Erigeron strigosus*	F	17.5	12.5	20	10	15.0
GACI	*Galium circaezans*	F	5	10	7.5	7.5	7.5
GAPU	*Gamochaeta purpurea*	F	10	12.5	5	5	8.1
GECA	*Geum canadense*	F	60	37.5	7.5	0	26.3
GERC	*Geranium carolinianum*	F	15	15	7.5	7.5	11.3
JUVI	*Juniperus virginiana*	T	25	30	27.5	40	30.6
LEVI	*Lespedeza virginica*	L	5	10	7.5	7.5	7.5
MYVE	*Myosotis verna*	F	12.5	7.5	10	2.5	8.1
PAPE	*Parietaria pensylvanica*	F	35	40	57.5	47.5	45.0
PAQU	*Parthenocissus quinquefolia*	V	57.5	45	60	62.5	56.3
QUMA	*Quercus marilandica*	T	7.5	15	2.5	0	6.3
QUMU	*Quercus muehlenbergii*	T	12.5	10	10	2.5	8.8
QUST	*Quercus stellata*	T	30	25	12.5	5	18.1
RHGL	*Rhus glabra*	S	17.5	22.5	10	10	15.0
SACA	*Sanicula canadensis*	F	12.5	12.5	2.5	2.5	7.5
SCPA	*Scleria pauciflora*	G	5	0	2.5	2.5	2.5
SCSC	*Schizachyrium scoparium*	G	25	12.5	10	5	13.1
SILA	*Sideroxylon lanuginosum*	T	10	15	5	10	10.0
SMBO	*Smilax bona-nox*	V	40	30	37.5	55	40.6
SYOR	*Symphoricarpos orbiculatus*	S	57.5	22.5	40	27.5	36.9
ULAM	*Ulmus americana*	T	52.5	60	57.5	52.5	55.6
ULRU	*Ulmus rubra*	T	10	5	10	12.5	9.4
VIRO	*Vitis rotundifolia*	V	12.5	32.5	17.5	20	20.6

All species that occur at least in 5% of plots are represented. Nomenclature follows USDA, NRCS, 2008. [a]Abbreviations for growth forms are: F=forb, G=graminoid, T=tree, S=shrub, L=legume,V=vine.

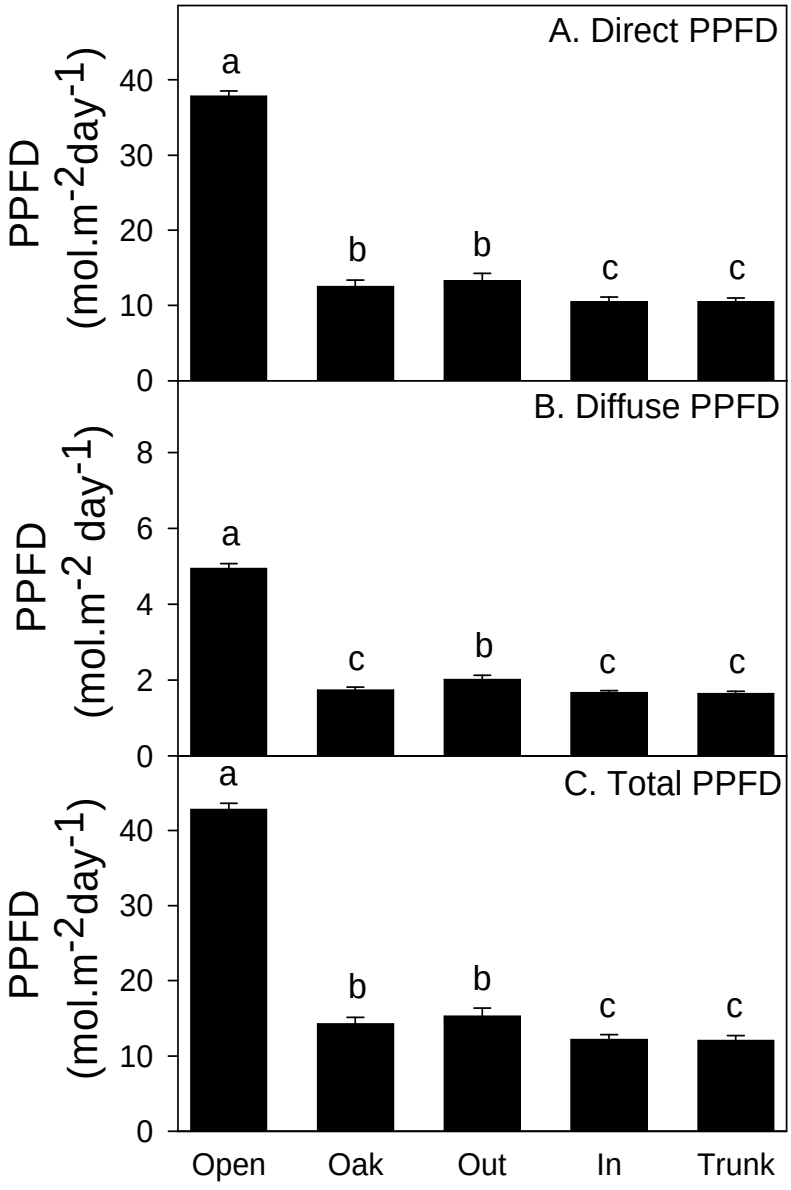

Fig. 1: Mean (±1 S.E.) A. direct, B. diffuse, and C. total photosynthetic photon flux density (PPFD) measured using analysis of canopy photographs. Letters indicate significant difference among treatments (Duncan's *post hoc*, α=0.05).

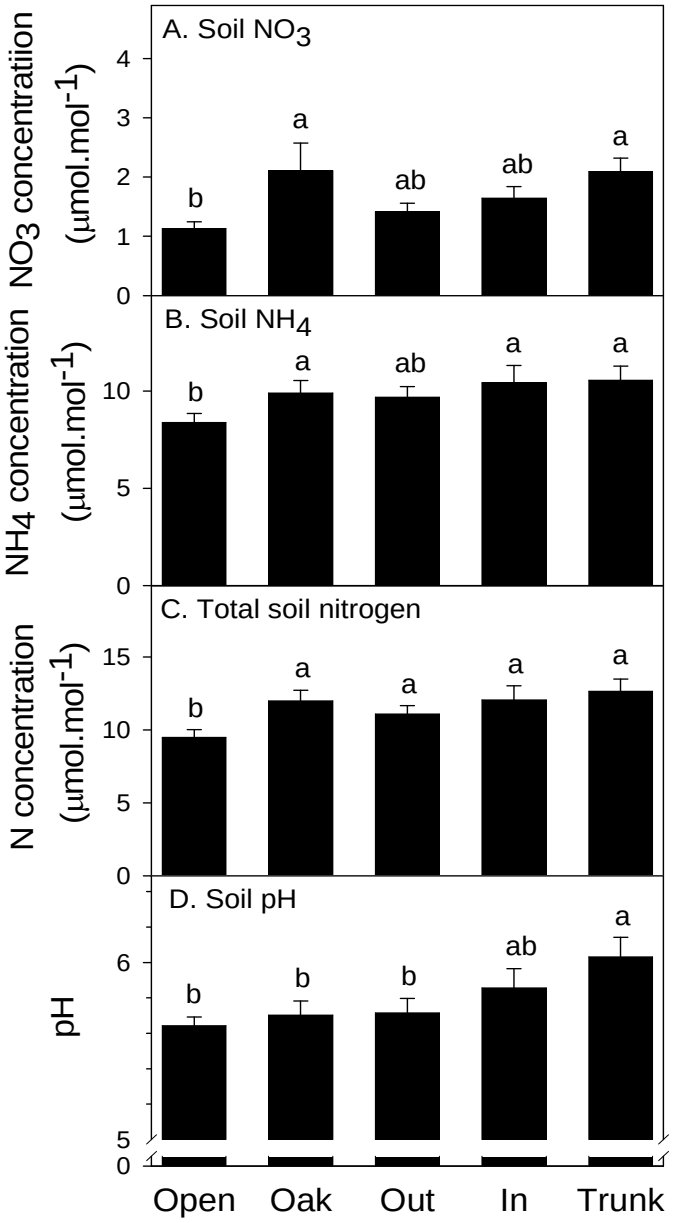

Fig. 2: Means (±1 S.E.) for soil A. nitrate, B. ammonium, C. total nitrogen, and D. pH. Letters indicate significant difference among treatments (Duncan's *post hoc* α=0.05).

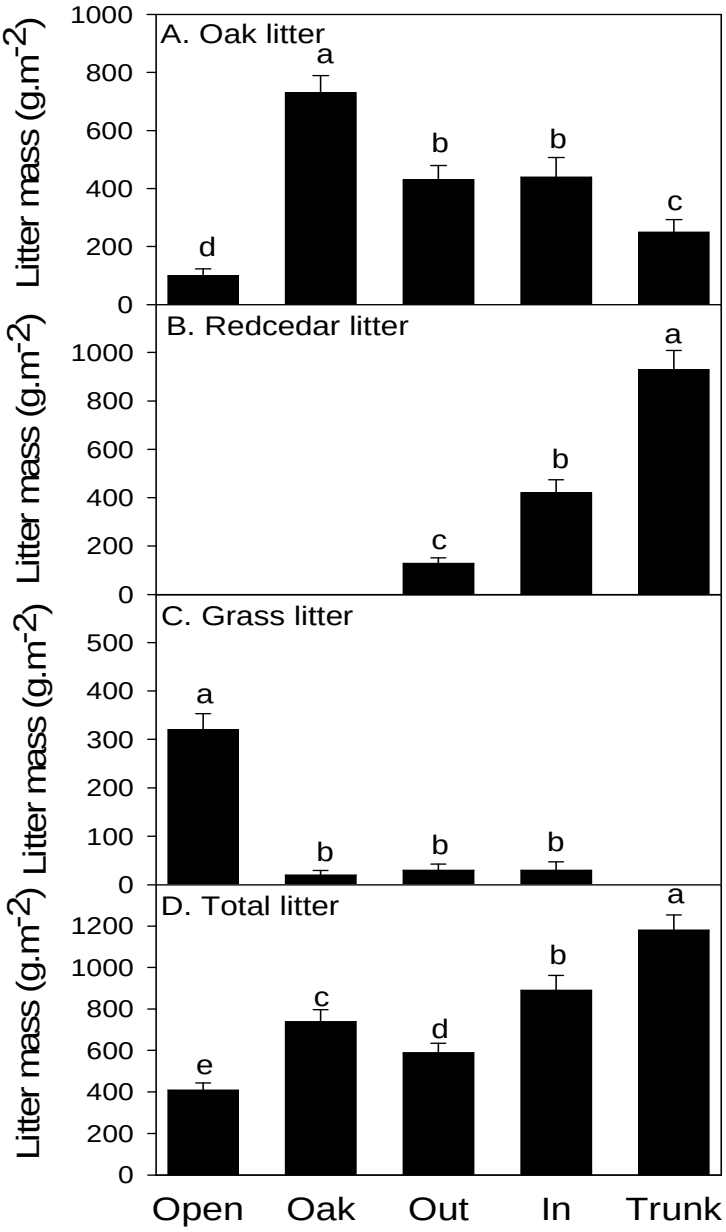

Fig. 3: Means (±1 S.E.) of A. oak, B. redcedar, C. grass, and D. total litter. Letters indicate significant differences among treatments (Duncan's *post hoc*, *P*=0.05).

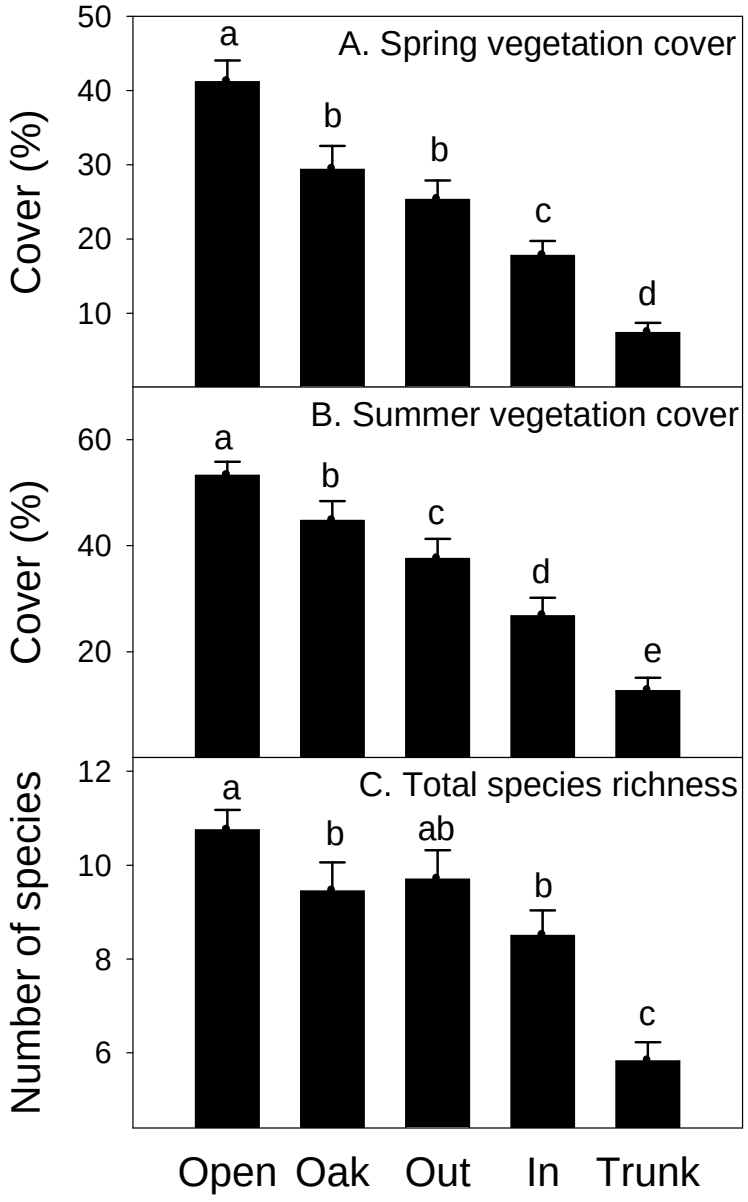

Fig. 4: Means (±1 S.E.) of A. spring and B. summer vegetation cover, and C. total species richness. Letters indicate significant differences among treatments (Duncan's *post hoc*, α=0.05).

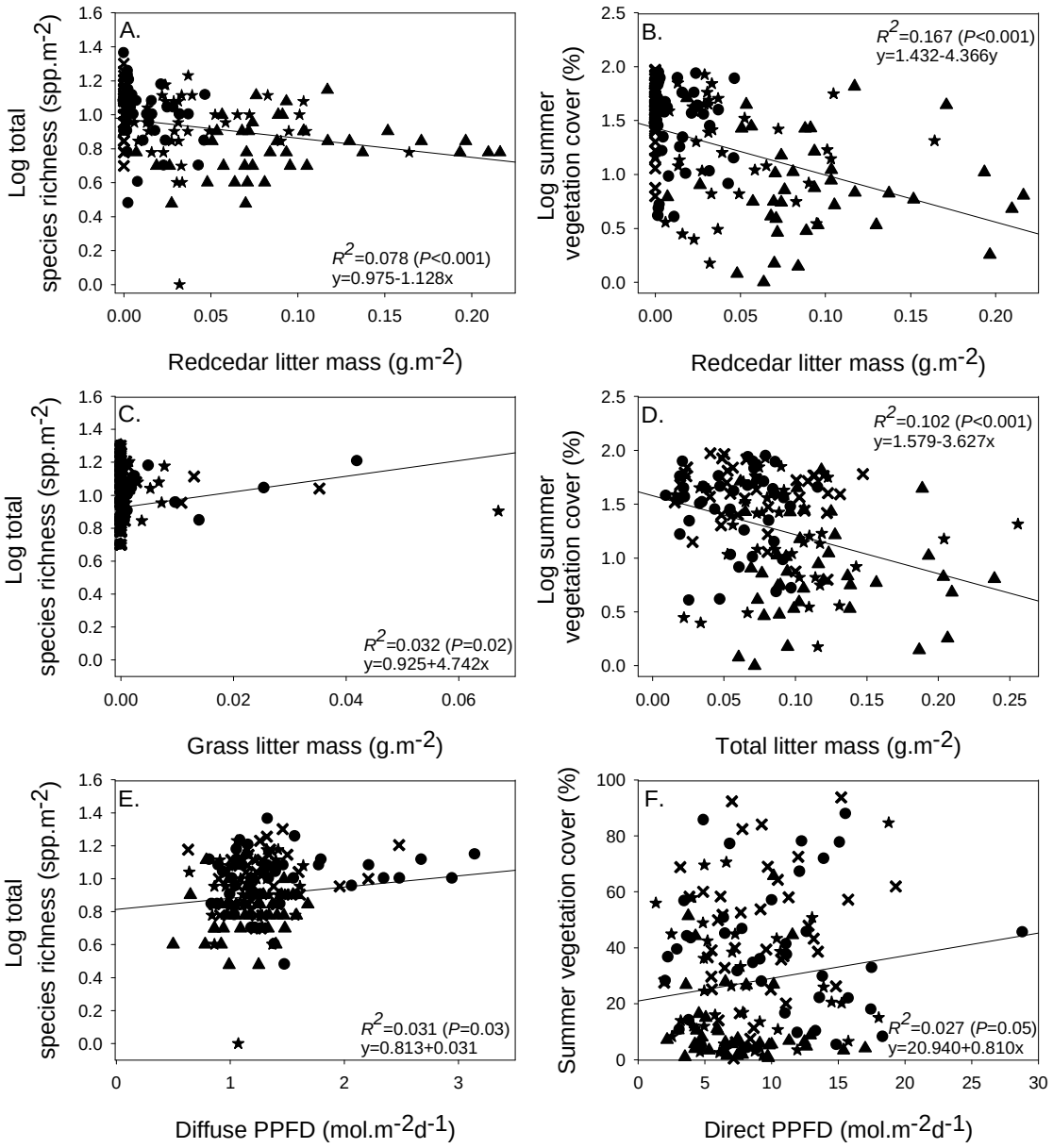

Fig. 5: Linear regressions of significant (α=0.05) variables with species richness and summer vegetation cover. Relationships between redcedar litter mass and A. species richness and B. summer vegetation cover are on the top, between C. grass litter mass and species richness and D. total litter mass and summer vegetation cover are in the center, and E. diffuse PPFD and species richness and F. direct PPFD and summer vegetation cover are on the bottom. Crosses represent oak plots, circles outer edge, stars inner edge and triangles trunk plots.

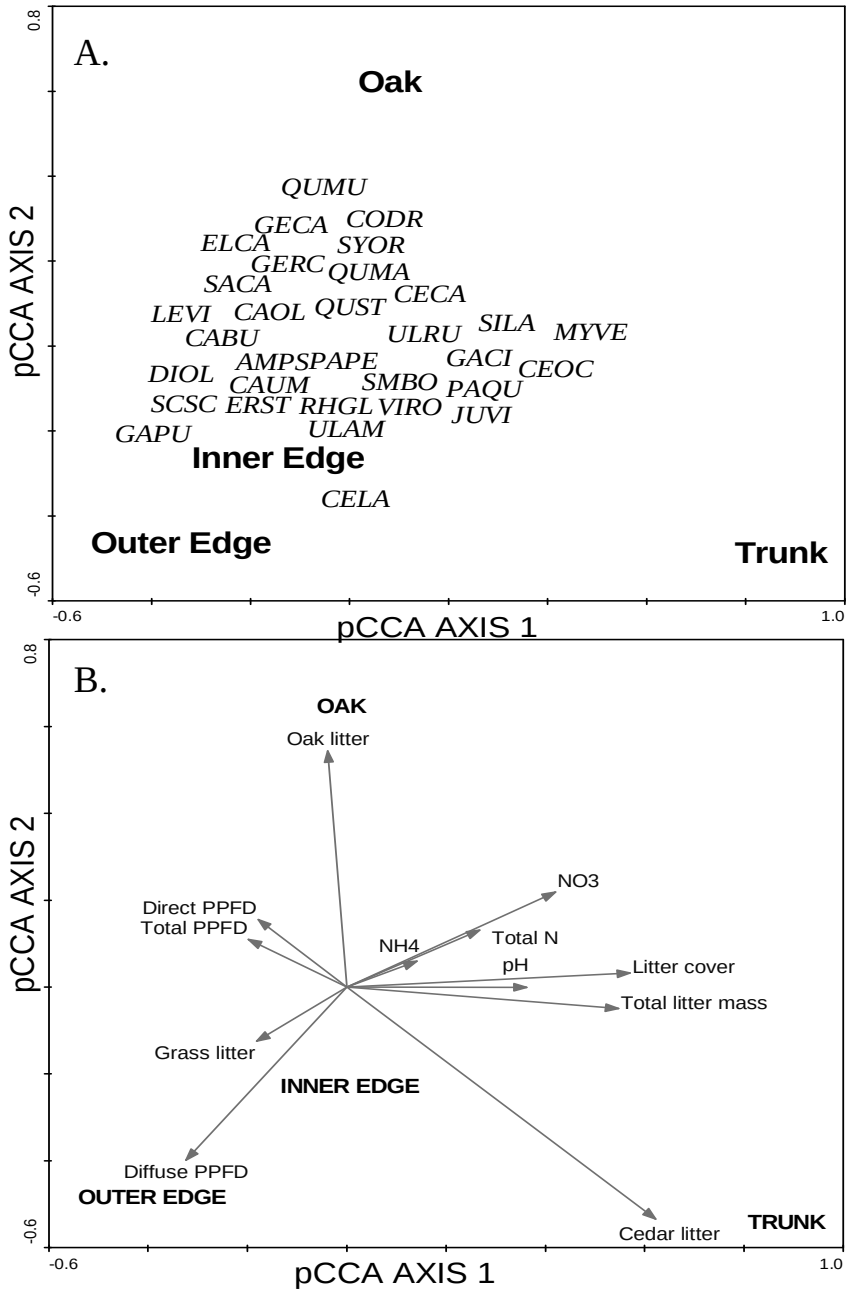

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Figure 6: A. pCCA biplot of species and categories. Bold letters represent treatments as centroids. Sites are included as covariables in blocks. Species codes (Table 2) may be slightly offset to increase visibility in diagram. First axis (λ=0.103) explains 61.5% of variability in species-environmental relation. Second axis (λ=0.050) explains 29.9%. B. biplot arrows for passive variables superimposed over the category centroids.

CHAPTER IV

EFFECTS OF *JUNIPERUS* ENCROACHMENT ON WINTERING BIRD COMMUNITY STRUCTURE IN OKLAHOMA CROSS TIMBERS FORESTS

ABSTRACT

I studied changes in avian wintering community composition, richness, and physiology due to encroachment of eastern redcedar (*Juniperus virginiana*) into the forest midstory of Cross Timbers forests in Payne County, Oklahoma, USA. I hypothesized that redcedar encroachment brings about changes in forest structure that affect species differentially, with insectivorous species showing increased body condition in redcedar-encroached forest relative to granivorous birds. I predicted that redcedar encroachment and consequent changes in forest structure would decrease avian richness and negatively influence species composition. I mist-netted birds and conducted transect counts at six sites (3 with >80% redcedar midstory, 3 with <10%) during 2007—2008. I calculated a body condition index of birds from morphometric measurements using principal component analysis (PCA). In 2008—2009, I conducted point counts in a 30 ha site with variable redcedar cover and used canonical correspondence analysis (CCA) to relate species abundance to environmental variables. Body condition was negatively correlated with redcedar canopy cover for my three focal species. Total species richness in the 30 ha site was negatively correlated with redcedar cover. Hermit Thrush and Golden-crowned Kinglet abundance was positively correlated with redcedar cover, whereas bark-probing birds as a guild showed a negative correlation. Two strong axes emerged from the CCA, one related to redcedar versus broadleaf cover, and the other to woody versus herbaceous understory cover. My results indicate that food was not limiting to focal species in encroached stands, and some species occurred in higher abundance in these stands.

However, the effects of redcedar on birds are species dependent, and bark-probing birds such as woodpeckers were negatively correlated with redcedar cover, possibly due to foraging impediments related to redcedar physical structure.

KEYWORDS Migratory birds, Body condition index, Eastern redcedar, Oklahoma, Cross Timbers

INTRODUCTION

Forest birds are highly responsive to changes in forest structure and diversity of forest microhabitat (James and Wamer 1982, Engstrom et al. 1984, Urban and Smith 1989, Provencher et al. 2002). Eastern redcedar (*Juniperus virginiana* L.) is a coniferous tree native to eastern North America that has become increasingly abundant in the prairies and forests of the southern Great Plains in recent decades (Engle et al. 2000) primarily because of anthropogenic fire suppression.

The effects of woody encroachment, including eastern redcedar encroachment, on prairie birds also have been well documented (Chapman 1996, Coppedge et al. 2001, Coppedge et al. 2004, Grant et al. 2004). Eastern redcedar encroachment in prairies increases avian species richness as shrubland and woodland birds such as Northern Cardinal (*Cardinalis cardinalis* L.) and Carolina Chickadee (*Poecile carolinensis* Audubon) expand their range due to development of woody cover. Certain neotropical migrants that depend on shrub cover in prairies may also benefit from redcedar encroachment (Coppedge et al. 2001). However, the integrity of avian communities has suffered with the intrusion of eastern redcedar into prairies. Typical grassland species such as Grasshopper Sparrow (*Ammodramus savannarum* Gmelin) and Western Meadowlark (*Sturnella neglecta* Audubon) decline with redcedar encroachment, possibly due to changes in 'visual cues that indicate unsuitable habitat' (Chapman 1996).

In Cross Timbers forests of northern Texas, Oklahoma, and southern Kansas, eastern redcedar can form dense midstories under a canopy of dominant post (*Quercus stellata* Wangenh.) and blackjack oak (*Q. marilandica* Münchh.) (Engle and Stritzke 1995). The increase of redcedar in these forests represents an alteration of forest structure because a dense midstory of a coniferous, evergreen tree replaces a fairly open midstory

with scattered deciduous shrubs. Structural changes in vegetation are more important in defining forest bird community composition and richness than changes in the species of vegetation present (Dickson et al. 1993, Sutter et al. 1995, Herkert 1997) and the formation of a dense redcedar midstory may be important in this respect. In addition to the changes in visual cues associated with redcedar encroachment, increases in redcedar reduce understory vegetation biomass (Smith and Johnson 2003, Linneman and Palmer 2006, Van Els et al. Chapter III). Reduced understory productivity and diversity can reduce foraging efficiency of ground-foraging birds (Rodewald and Smith 1998). However, the effects of eastern redcedar on bird assemblages through alterations in forest structure may not solely be negative. The dense structure of redcedar-encroached forests may offer increased cover and may harbor more insect prey (Norberg 1978, Danks 1991). In forests and woodlands, the most marked effects of tree species on bird species composition have been noticed between coniferous species and broadleaf trees (Franzreb 1978). Eastern redcedar differs from deciduous angiosperms in that it bears conelets ('berries') which form an important food source for some bird species in winter (Horncastle et al. 2004) and because its persistent foliage provides visual and thermal protection in the winter.

The effects of an eastern redcedar midstory development in forests on bird communities have not received much attention compared to the effects of redcedar encroachment on prairies and grassland birds. However, changes in forest bird communities may be important and may affect a large geographical area. Cross Timbers forest, where redcedar encroachment is particularly prevalent, occupies approximately 79,000 km^2 (Kuchler 1964) and represents an important breeding area for many forest bird species, but also, due to their relative southern location for temperate forests, an important wintering area for several North American short-distance migrants. The effects of forest structure on behavior and distribution of birds may be particularly pronounced during winter, when climatic and nutritional stresses are greater than during any other time of year (Desrochers et al. 1988, McNamara and Houston 1990). Redcedar is the only abundant evergreen tree species in most of the Cross Timbers forests. This accentuates habitat structure differences in winter between forests made up of only deciduous species and those with a coniferous midstory. Winter conditions are thus ideal for investigating

spatial distribution, habitat selection and the resulting physical effects on forest-dwelling birds. ,

The objectives of this study were to determine the effects of increasing redcedar encroachment on wintering bird community composition, structure, and physiology in Cross Timbers forests of central Oklahoma. I hypothesized that a denser structure in forests due to redcedar encroachment negatively affected species that favor open forests or savannas while species associated with dense forest structure increase with redcedar abundance. To investigate the influence of redcedar encroachment on avian physiology, I selected three focal species and hypothesized that Yellow-rumped Warblers (*Dendroica coronata* L., mainly insectivorous/berry-eating) and Red-breasted Nuthatch (*Sitta canadensis* L., mainly insectivorous, eats conifer seeds in wintering habitat) would show higher body condition in redcedar-encroached forest than in forests with little redcedar, whereas Dark-eyed Juncos (*Junco hyemalis* L., mainly granivorous) would show lower body condition. I also predicted that, based on habitat selection, insectivorous and berry-eating species would be more abundant in redcedar-encroached forest than granivorous and omnivorous species.

METHODS

Study sites

I conducted this study at seven locations in western Payne County, Oklahoma. The study locations lay at the western edge of the Cross Timbers forest which forms an ecotone between the tallgrass prairie and eastern broadleaf forests. All locations had a variable overstory of *Quercus stellata* and *Q. marilandica*, which are the dominant tree species in the area. Some had a variable midstory of *Juniperus virginiana*. I excluded large gaps and forest edge. Additional tree species included *Q. muehlenbergii* Engelm., *Sideroxylon lanuginosum* Michx., *Celtis occidentalis* L., *C. laevigata* Willd. and *Ulmus americana* L. Understory vegetation in winter was characterized by vines such as *Smilax bona-nox* L., *Vitis rotundifolia* Michx.. *Parthenocissus quinquefolia* L., the woody shrub *Symphoricarpos orbiculatus* Moench. and the senesced grasses *Schizachyrium scoparium* (Michx.) Nash. and *Dichanthelium oligosanthes* Gould.

Study 1 - Effects of redcedar encroachment on physical condition and abundance

I sampled a ~2 ha circular location (80 m radius) at each of six sites from Oct.–Mar. 2007–2008. Three of these six locations had a dense redcedar midstory (>80% relative cover, i.e. 80% of sky obstructed by redcedar cover) with a small broadleaf component (36.1150, -97.1949; 36.1017, -97.2070; 36.1175, -97.2126) and the other three had low relative redcedar cover (<10%) with a high broadleaf component (36.1113, -97.1920; 36.1083, -97.2107; 36.1076, -97.2273).

I used mist nets to capture wintering songbirds in Oct—Mar 2007—2008, a time span suitable for sampling wintering birds in most of North America (Kricher 1975). At each banding station, I operated four mist nets (6 m, 30 mm mesh) spaced approximately 20 m apart. I did not clear vegetation to accommodate a standard array and used available space between trees for net placement. By doubling the height of net poles, I placed one net higher (approximately 5 m to the top of the net), to capture birds near canopy level (Bonter et al. 2008). The other three nets were placed at ground level. To increase capture rates by attracting foraging flocks, I broadcast calls of wintering songbirds through a battery-powered speaker attached to an MP3 player. I captured birds during the 3 hrs after dawn or before dusk. I adjusted my sampling to correct for seasonal variation in sunrise and sunset. I sampled each of six sites ten times (once every two weeks). Rainy and windy conditions (>10 kph) were avoided.

I immediately weighed captured birds in a cloth bag using a spring scale calibrated to the weight of the bag (±0.5 g), and marked them with USFWS numbered metal bands. I visually estimated subcutaneous fat deposits on a 0-3 scoring system (Helms and Drury 1960). I also determined unflattened wing chord using a ruler (±1 mm) and tarsal length and culmen length using dial calipers (±0.1 mm). I sexed and aged birds considering morphometric characteristics and plumage details (Pyle 1997).

I analyzed capture data for three focal species (Yellow-rumped Warbler, Dark-eyed Junco, and Red-breasted Nuthatch) of which I captured at least ten individuals. I calculated body condition indices from tarsal length, culmen length and wing chord using regression and Principal Components Analysis (PCA) in order to create a useful body condition statistic for comparison between forests with variable amounts of redcedar and among species. For this purpose, residuals (i.e. deviation of an individual's mass given

morphometric measurements) were used as a body condition index (Rodewald and Shustack 2008a, 2008b). I calculated differences in body condition index and subcutaneous fat between forests with much and little redcedar using T-tests, and differences in gender and age using Pearson's Chi-square tests. For comparison between forest types, I assumed that most species in my study were sedentary in winter, as has been shown for several species included in this study or related species (Kilham 1958, Condee 1970, Salomonson and Balda 1977, Enoksson and Nilsson 1983, Brown et al. 2002). However, I recognize that some species move locally, especially early and late in the season. I used SPSS version 16.0 (SPSS 2007) statistical software for these tests, with α=0.05.

To determine species richness and composition, a single observer conducted ten 30 min timed area searches at each circular location during the winter of 2007—2008. All observations were completed during the first three hours after sunrise or the last three before sundown. During the winter 2008–2009 season, I used modified sampling to provide an unbiased estimator of abundance. At each of the six sites, a single observer surveyed a 500 m transect on eight separate occasions. Transects bisected the circular locations, extending beyond the location into similar habitat (Bibby et al. 2000). The observer recorded the position of each bird detected as an orthogonal distance to the transect (Emlen 1971) using a rangefinder (Bushnell Co.). Transect counts were completed during the first two hours of the morning or the last two hours of the afternoon. From the orthogonal distance to transects observed in the field, I calculated a detection coefficient based on a lateral distance of 125 m (coefficient of detectability, $CD_{125,}$ Emlen 1971) from transects; a method that is suitable for non-vocalizing wintering birds. I calculated CD values for both oak-dominated and redcedar-encroached forests, assuming that structural differences in the two habitat types would lead to differences in detectability. I then applied coefficients of detectability from 2008–2009 data to my 2007–2008 data to compare inter-annual variation in bird abundance. I only report CD_{125} values for species that were detected with greatest frequency in two proximal strips of 30 m along transects. Larger species such as corvids yielded unrealistic CD_{125} values because they were most frequently recorded at a distance >60 m from the observer, I omitted these species from my analysis.

Within the six circular locations first sampled in 2007—2008, I measured vegetation in one central circular plot (15 m) and four smaller plots (5 m radius) that were 40 m from the center in each cardinal direction. I measured canopy cover using a digital camera with a hemispherical fisheye lens. During late March (leaf-off), I took nine hemispherical photographs at each 15 m plot, one at the center, and at 5 m and 10 m away from the center in each cardinal direction. I calculated canopy openness and tree cover (broadleaf/redcedar as a percentage of total cover) using grayscale and full color analyses respectively in WinScanopy and XIScanopy software (Régent Instruments 2006). In grayscale analysis, the colors in the picture were divided into two groups, black (canopy) and white (sky), based on manual categorization of proximity to either color extreme. In full color analysis, I set three color classifications and distinguished between dark green and rufous brown (redcedar), other greens and browns (broadleaf trees) and light colors (sky).

Study 2 – Avian species relationships with redcedar and other environmental variables

The following year (Oct.–Mar. 2008–2009), I set up 63 plots in one rectangular 30 ha site (36°04', -97°21'). Circular plots had a radius of 20 m and were arranged in a 7 x 9 cell grid. All plot centers were located at least 40 m from the forest edge and 60 m from each other. Midstory redcedar cover at the 30 ha site varied from 0% to 70%. In the 30 ha site, the same observer performed 2 min point counts at all 63 plots. I finished point counts within 4 hrs after sunrise. I excluded from analysis birds that flew over and did not make use of the habitat.

Within the 30 ha site, I took five hemispherical photographs at each grid point, one at the center, and one at 12 m away from the center in each cardinal direction. I took all pictures in March during leaf-off. In addition, I used a Basal Area Factor (BAF) 10 angle gauge to estimate tree basal area for each point and I determined height (±10 cm) of the three tallest deciduous trees and three tallest redcedars in the count circle using a Haglöf Vertex Hypsometer (Haglof Inc.).

To quantify understory vegetation, I used 20 m transects in each cardinal direction from the center of the point count circle. I determined length of vegetation cover by plant functional forms (forb, grass, vine, shrub) and length of litter cover along tape measures

(± 1 cm) according to the line-intercept method (Canfield 1941). I then translated these data into relative cover. At five points spaced at regular 4 m intervals along transects, I measured maximum vegetation height and litter depth with a ruler (±1 mm).

I performed a series of linear regressions (α=0.05) to determine relationships between environmental variables and avian species abundance in my grid count. Environmental variables included height, cover and basal area of redcedar and broadleaf trees, cover of different functional groups of understory vegetation (senesced grasses, senesced forbs, vines, saplings below 1.38 m), and leaf litter. I chose these understory variables because there is a negative relationship between redcedar cover and cover of herbaceous vegetation (Engle et al. 1987; Linneman and Palmer 2006) and understory vegetation may be important to wintering birds in terms of nutrition and cover. I applied regressions to both individual species and avian functional groups, including bark-probers (woodpeckers and nuthatches), leaf litter specialists such as American Woodcock (*Scolopax minor* Gmelin), Spotted Towhee (*Pipilo maculatus* Swainson), and Rusty Blackbird (*Euphagus carolinus* Mueller); seed-eaters (emberizids and finches), berry-eaters (i.e., thrushes, Cedar Waxwing [*Bombycilla cedrorum* Vieillot] and Yellow-rumped Warbler) and insectivorous birds (wrens, Yellow-rumped Warbler, kinglets). I used Canonical Correspondence Analysis (CCA) to examine avian composition in relation to all environmental variables (Ter Braak 1986). To ensure randomization of location between transect samples I applied toroidal shifts (Diggle 1983). I included only species that occurred in more than 5% of all counts to avoid bias of species that occur in only one or a few plots with microhabitats which may not be typical for them. I used CANOCO for Windows 4.5 (Ter Braak and Šmilauer 2002) for all ordination analyses. Furthermore, I calculated Ivlev's electivity indices (Ivlev 1961) to explore electivity of redcedar and broadleaves by all species. The index was traditionally used to calculate food preferences (Ivlev 1961), but is used increasingly for habitat selection as well (Storch 1993, Blackwell and Krohn 1997). $E_i=r_i-p_i/r_i+p_i$ is the equation that defines electivity (E_i), where r_i represents the percentage of habitat (i) used by a species and p_i is the percentage of habitat that is available to a species.

RESULTS

Site characteristics

In the three sites with <10% redcedar cover, *Quercus stellata* contributed on average 52.7% to total basal area (BA); *Q. marilandica* 30.7%, other hardwoods 13.9%, and *Juniperus virginiana* 2.7%. For sites with >80% redcedar cover, *J. virginiana* contributed 75.2% to BA, *Q. stellata* 22.5%, *Q. marilandica* 1.7% and other hardwoods 0.6%. Total basal area varied little between the two site types, and was 24.8 $m^2.ha^{-1}$ in high redcedar sites and 24.7 $m^2.ha^{-1}$ in low redcedar sites. *Q. stellata* had consistently the greatest mean DBH and height (Table 1).

Study 1 - Effects of redcedar encroachment on physical condition and abundance

I captured 89 individuals of 12 species, of which only Dark-eyed Junco, Yellow-rumped Warbler, and Red-breasted Nuthatch could be used to make meaningful comparisons between habitats. In calculating body condition indices, the first principal component explained 44.5% of variation among Dark-eyed Junco individuals (λ=1.335), 47.2% among individuals of Yellow-rumped Warbler (λ=1.416), and 54.3% among individuals of Red-breasted Nuthatch (λ=1.630). Dark-eyed Junco (P<0.01), Yellow-rumped Warbler (P=0.05) and Red-breasted Nuthatch (P<0.01) captured in forests with a redcedar-midstory had lower body condition indices than in forests with little redcedar. Pooled scores for all winter residents (i.e. excluding year-round species) captured in forests with a redcedar-midstory also showed a lower subcutaneous fat score (P<0.05) than those caught in forests with little redcedar, but body condition indices did not differ (P=0.48). Body condition indices of Dark-eyed Junco (r^2=0.31, P<0.01), Red-breasted Nuthatch (r^2=0.56, P<0.01), and Yellow-rumped Warbler (r^2=0.39, P<0.01) were negatively correlated with redcedar canopy cover.

Body condition index scores pooled for all winter resident species showed an increasing trend with the progression of winter in both redcedar-encroached forest and forest with little redcedar, as did subcutaneous fat. Dark-eyed Junco (P=0.02) and Yellow-rumped Warbler (P=0.04) showed greater fat deposits during the second half of winter than during the first half. There was no difference for Red-breasted Nuthatch (P=0.16). Genders of Yellow-rumped Warbler (χ^2=1.644, n=19, P>0.10), Dark-eyed

Junco (χ^2=0.269, n=21, *P*>0.10) and Red-breasted Nuthatch (χ^2=0.351, n=11, *P*>0.10) were equally distributed over the two habitat types. Juveniles and adults of Yellow-rumped Warbler (χ^2=2.011, n=19, *P*>0.10) and Red-breasted Nuthatch (χ^2=0.196, n=11, *P*>0.10) were equally distributed over habitats, whereas juveniles and adults of Dark-eyed Junco were not (χ^2=3.103, n=21, *P*=0.04). Adult Juncos were captured more frequently (n=8) in redcedar than juveniles (n=3), whereas juveniles (n=6) were more frequently caught in deciduous habitats than adults (n=3).

Species abundance

I applied CD_{125} values to my count data to obtain avian abundance data. Species abundance among the six circular locations was highly variable within as well as between the two consecutive winters (Table 2). Tufted Titmouse (*Baeolophus bicolor* L.) and Carolina Wren (*Thryothorus ludovicianus* Latham) were the only species more abundant at the three sites with <10% redcedar, whereas Hermit Thrush (*Catharus guttatus* Pallas), Yellow-rumped Warbler, and Golden-crowned Kinglet (*Regulus satrapa* Lichtenstein) were more abundant in forests with >80% redcedar. Dark-eyed Junco and Golden-crowned Kinglet showed great inter-annual variation in abundance among sites. The abundance trends for these species over the two years did not follow the same trend; Dark-eyed Junco was more common in 2007—2008 in both the high and low redcedar sites, whereas Golden-crowned Kinglet was more common the next winter in redcedar. Other species showed inter-annual variation only in one site type, Tufted Titmouse and Carolina Chickadee were more common at sites with <10% redcedar in 2007—2008 than in the following winter and Ruby-crowned Kinglet (*Regulus calendula* L.) was more abundant at sites with >80% redcedar in 2007—2008 than the next winter. Abundance of Yellow-rumped Warbler and Hermit Thrush showed little inter-annual variation at either site type.

Study 2 - Species relations with redcedar and other environmental variables

Total species richness was negatively correlated with relative redcedar canopy cover (R^2=0.09, *P*=0.02), and declined from about 15 species at 0% encroachment to 12 species at 90% encroachment. No relationship between redcedar cover and overall abundance

(number of individuals/plot with 40 m diameter) (P=0.22) was found. Of all individual species in the study, regression showed significant, positive correlations between redcedar cover and abundance of Hermit Thrush (R^2=0.14, P=0.002) and Golden-crowned Kinglet (R^2=0.26, P<0.001), and negative correlations between redcedar canopy cover for Fox Sparrow (*Passerella iliaca* Merrem, R^2=0.18, P=0.001), Red-bellied Woodpecker (*Melanerpes carolinus* L., R^2=0.31, P<0.001), Red-headed Woodpecker (*M. erythrocephalus* L., R^2=0.23, P<0.001) and White-breasted Nuthatch (*Sitta carolinensis* Latham, R^2=0.20, P<0.001) abundance. Cumulative regressions of 'bark probing', berry-eating and insectivorous bird abundance (Fig. 1) also yielded significant relationships with redcedar cover.

Canonical correspondence analysis identified two strong axes (Fig. 2). The main axis was related to a gradient of redcedar encroachment in broadleaf forest. The other axis explained only less than half of the variation of the first axis and was related to woody understory cover (mostly vines) versus herbaceous understory cover (mostly grasses). Species were mostly found in the central area of the CCA diagram, away from the environmental centroids. This area lay approximately halfway between the redcedar and broadleaf centroids, confirming that most species I found were generalists. However, species points of most woodpeckers, Rusty Blackbird, and White-breasted Nuthatch were closer to the broadleaf centroid than to the redcedar centroid, whereas the opposite was true for Hermit Thrush and Golden-crowned Kinglet. Spotted Towhee and Carolina Wren were located relatively close to the vine centroid. When I placed greater than mean species abundance points in a diagram with redcedar and broadleaf cover on the x and y axis respectively (Fig. 3), most resident species, except three bark-probers, were centered at a redcedar/broadleaf proportion of 20-40%/20-40%.

Yellow-rumped Warbler and Dark-eyed Junco showed weak electivity for low broadleaf and low redcedar cover, while Hermit Thrush and Golden-crowned Kinglet showed weak positive responses to high redcedar cover and strong positive responses to low broadleaf cover (Fig. 4). Red-bellied and Red-headed woodpeckers showed a strong negative response to medium and high redcedar cover.

DISCUSSION

Body condition differences with different amounts of redcedar cover

Body condition indices of Yellow-rumped Warblers, Red-breasted Nuthatches, and Dark-eyed Juncos, as well as subcutaneous fat of all winter resident species, were lower for birds wintering in forests with a midstory of redcedar relative to birds in forests with little redcedar. In general, wintering bird abundance is positively related to resource availability (Pulliam and Brand 1975, Dunning and Brown 1982, Meehan et al. 2004). Intuitively, lower body fat does not correspond with the relatively high abundance of some species in redcedar-encroached habitat. However, several studies have reported that body fat was inversely related to food availability (Rogers 1987, Rogers and Smith 1993, Strong and Sherry 2000) indicating that redcedar-encroached forest may offer increased nutrition for the species with lower body condition relative to forests without redcedar. Birds in low quality habitats may respond to an increased potential of sudden food shortage by maintaining high body fat, whereas birds in higher quality habitat, where the possibility of a sudden food scarcity event is lower, do not have the need to store excess fat. Lower fat levels in wintering birds also go hand-in-hand with lower vulnerability to predation (Lima 1986) and lower metabolic energy demands (Meehan et al. 2004), which may be an increased advantage for certain bird species wintering in redcedar-dominated habitats.

There may be important thermal and nutritional advantages to wintering in forests with a dense redcedar component. Juniper berries are a common to exclusive nutrition source for many wintering bird species (Phillips 1910, Paddar and Lederer 1982), and redcedar berries can be an excellent food source. Redcedar berries provide a combination of high protein and energy content (Smith et al. 2007). Their high protein content contrasts with acorns and other fruits of non-leguminous angiosperms (Short and Epps 1976) found in the Cross Timbers. Redcedar berries may represent an important source of protein for birds during winter, when the availability of other sources of protein such as insects becomes more sporadic. In contrast with oaks and other broadleaves, redcedar berries as a food source are available to birds throughout fall and the winter season (Phillips 1910). Borgmann et al. (2004) showed that fruit-bearing shrubs determined Yellow-rumped Warbler abundance and that warblers actively track fruit abundance. In

contrast, the potential nutritional advantage of redcedar to woodpeckers and other species may be negligible because they do not generally consume redcedar berries.

Redcedar stands also may provide thermal refuge for wintering birds. Conifer stands had increased ambient temperatures compared to stands of deciduous trees during cold winter weather (Petit 1989) and were therefore favored by birds during adverse weather conditions. Black-capped Chickadee (*Poecile atricapillus* L., Odum 1942) and American Robin (*Turdus migratorius* L.) are known to roost in dense conifer foliage in winter, although energy saved by the latter compared to roosting in the open was only 4% (Walsberg and King 1980). Lower body mass in wintering birds is directly related to higher ambient temperature (Lima 1986). Redcedar may thus serve as a foraging or roosting refuge for birds on cold days.

Yellow-rumped Warblers captured in areas with >80% redcedar cover during my last 10 sampling days in February/March had fat scores ≥2 which was higher than earlier in the winter (n=3). This may be caused by premigratory hyperphagia, a period of increased nutritional intake just before migration (Odum 1960). Mean body mass, fat and body index data for the species would suffer from a positive bias, if these late individuals had increased levels of subcutaneous fat due to a brief period of premigratory hyperphagia. However, even with these saturated individuals, Yellow-rumped Warblers captured in areas with >80% redcedar were still leaner than birds from the mainly deciduous habitat. Moreover, hyperphagia would confirm that areas with large amounts of redcedar offer increased foraging potential, due to the possibility for birds to put on mass in a limited amount of time. No difference was noticed between fat deposits in the last two weeks of the capture period and the previous month for any other species indicating that most species did not exhibit premigratory hyperphagia.

No differences were found in gender of Dark-eyed Junco, Yellow-rumped Warbler and Red-breasted Nuthatch in forests with much and little redcedar. I did, however, detect age differences; adult juncos were more common in redcedar-dominated forest, whereas the opposite was true for broadleaf-dominated forests. Considering that birds may select redcedar-encroached habitat because of nutritional advantages, this may indicate that subordinate juvenile birds are driven out of the redcedar-encroached habitat by the adults. Although it is well established that gender influences wintering distribution

of Dark-eyed Juncos (Ketterson and Nolan 1976), age may also be a crucial factor in defining junco distribution. Age determines rank in Yellow-eyed Juncos (*Junco phaeonotus palliatus*) (Moore 1972) and is one of the determinants in establishing dominance as defined by interactions between wintering Dark-eyed Juncos (Ketterson 1979).

I do not have data on body condition for several species that were more abundant in forests with little redcedar encroachment, including woodpeckers. This lack of data prevents us from investigating body condition differences between species of guilds with highly differentiated foraging and roosting strategies. Differences among wintering avian guilds in fat deposition can be significant (Rogers 1987) and these may affect generalized conclusions about body condition in relation to nutrient availability and the resulting habitat quality.

Species distribution and abundance differences

Parallel to declines in avian species richness with encroachment by redcedar in grasslands (Chapman 1996), I found a small decrease in total number of species in forests with increased redcedar cover. However, it seems that the compositional shift in species recorded by Chapman in prairies, whereby prairie specialists are replaced by woodland generalists at low redcedar encroachment levels, does not occur for wintering birds in redcedar-encroached forests. The less frequent migratory species showed a greater spread over different combinations of redcedar/broadleaf composition than did resident species. Similar to this, Holmes and Robinson (1981) showed that uncommon and edge-of-range species depended on specific tree species more than common species for foraging. This agrees with my finding that most resident species and the most abundant migratory species relied on a habitat that contained a mix of redcedar and broadleaf trees, which may be an indication of the generalist foraging behavior of these species.

In contrast, I observed a negative correlation between redcedar and bark-probing birds based on the results of the CCA, the redcedar/broadleaf diagram, and by electivity indices. Red-cockaded Woodpeckers (*Picoides borealis*) select taller stems in forests with midstory vegetation than in forests without a midstory or in forest gaps (Rudolph et

al. 2002). Also, most wintering birds are highly responsive to temperature differences caused by changes in incoming solar radiation or wind and move to lower forest strata with denser substrates when conditions are unfavorable. Female Downy Woodpeckers and White-breasted Nuthatches however did not participate in this vertical migration and instead selected the leeward side of large-diameter stems to protect themselves from the cold (Grubb 1977). The exact mechanisms that drive this avoidance of lower-level vegetation of bark-probing species are unknown but may be related to lower foraging potential and mobility in areas with dense foliage. Redcedar may thus cause both resident and migratory woodpeckers and nuthatches to avoid lower forest strata. Additionally, the deciduous forest, mainly composed of oaks in my region, may be beneficial to the physical condition of woodpeckers and other species because of greater stem size for cavity nesting or due to more cavities offering nocturnal insulation than in redcedar-encroached forest (Kricher 1975).

The weak positive statistical relationships between redcedar cover and insectivorous and frugivorous species were largely a result of the inclusion of Hermit Thrush and Golden-crowned Kinglet, as their abundance patterns were related to redcedar and corresponded with results from the CCA. Electivity indices however showed that these species' distributions are not defined by the selection of redcedar habitat, but more so by the avoidance of high broadleaf cover. Wintering Hermit Thrushes are at least locally more abundant in stands of pine than in broadleaf stands (Brown et al. 2002) and wintering Golden-crowned Kinglets are range-wide more abundant in moist, coniferous forests than in broadleaf-dominated forests (Lepthien and Bock 1976). There seem to be similarities between breeding habitat and wintering habitat structure for both of these species, which may have an effect on these species' abundance patterns in redcedar-encroached forests. Yellow-rumped Warbler also was more common in redcedar-encroached sites during both winters. However, theses individual abundance patterns did not correspond with outcomes from the CCA analysis and with the location in Fig. 3, where the species is located at points of equal redcedar/broadleaf cover. Electivity indices show that Yellow-rumped Warbler avoids closed redcedar-encroached and broadleaf-dominated forests. Yellow-rumped Warbler thus seems to respond to redcedar encroachment on a fine scale, but not on a broad scale. As long as there is sufficient

broadleaf cover, this species does not show any changes in abundance with increasing redcedar.

There was considerable annual variation in species abundance, with 2007—2008 clearly showing greater numbers and richness of birds than 2008—2009. Red-breasted Nuthatch was common in 2007-2008 and nearly absent in 2008—2009, which indicated that 2007-2008 was part of an invasion winter for this and perhaps other species. Most species, however, exhibited no inter-annual abundance changes between redcedar-encroached forest and forest with little redcedar. Although I only have data for two years, this may mean that the distribution of species over the two habitat types may be fairly consistent among different winters, although changes in abundance across habitats may be present.

The effects of redcedar encroachment on wintering forest birds are variable and species-specific. Body condition data in this study may give us some clues as to why certain species react positively or neutrally to redcedar, but a greater sample size and measurements from more species would be valuable to further explore the impacts of redcedar on avian forest communities. However, redcedar in forests has the potential to alter avian species composition and abundance patterns. While generalist forest species may show no abundance changes, the structural changes that redcedar brings to Cross Timbers forests may come to the benefit of certain insectivorous and frugivorous migrants and at the expense of both resident and migratory woodpeckers. As redcedar continues to increase in Cross Timbers forest stands, populations of conservation priority species that use these stands should be carefully monitored.

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Table 1: Mean basal area, diameter at breast height, and tree height (±S.E.) of three sites with <10% redcedar cover and three with >80% cover. DBH=Diameter at Breast Height.

Tree species	Sites with <10% redcedar cover			Sites with >80% redcedar cover		
	Basal Area ($m^2.ha^{-1}$)	DBH (cm)	Height (m)	Basal Area ($m^2.ha^{-1}$)	DBH (cm)	Height (m)
J. virginiana	0.66±0.16	25.91±5.96	5.61±0.75	18.57±0.08	29.29±1.57	7.05±0.18
Q. stellata	13.07±0.03	36.06±1.19	8.49±0.24	5.56±0.15	36.58±4.37	8.40±0.58
Q.marilandica	7.61±0.04	34.65±1.85	7.50±0.40	0.42±0.09	18.47±4.87	3.31±0.61
Others	3.45±0.04	24.88±1.79	6.14±0.36	0.15±0.03	31.67±7.58	5.65±0.85

Table 2: Mean species abundances (±S.E.) along transects 500 m in length and covering a lateral area of 125 m at sites with variable amounts of redcedar cover for the winter seasons of 2007—2008 and 2008—2009. *Represents no observations. Avian species abbreviations throughout text follow four-letter alpha codes proposed by Pyle and DeSante (2006). CACH=Carolina Chickadee, CARW=Carolina Wren, DEJU=Dark-eyed Junco, ETTI=Tufted Titmouse, GCKI=Golden-crowned Kinglet, HETH=Hermit Thrush, MYWA=Yellow-rumped (Myrtle) Warbler,NOCA= Northern Cardinal, RCKI=Ruby-crowned Kinglet.

Species abundance	Relative redcedar cover (%)					
	7.6	8.2	8.7	81.2	87.2	92.7
CACH 2008	9.7±0.5	16.8±0.7	26.8±2.4	9.6±1.1	6.8±1.6	5.5±0.6
CACH 2009	1.9±0.3	0.8±0.1	4.1±1.1	4.1±0.8	1.4±0.3	0.7±0.6
CARW 2008	3.1±1.3	6.3±0.3	3.1±0.3	2.7±0.3	1.8±0.3	2.7±0.3
CARW 2009	*	0.6±0.4	2.5±0.2	1.3±0.8	1.3±0.2	0.9±0.6
DEJU 2008	28.7±2.5	23.9±2.6	11.4±0.5	20.2±4.3	34.3±1.4	20.3±2.7
DEJU 2009	0.6±0.6	1.8±1.5	3.0±2.5	7.6±2.5	10.2±1.9	12.7±2.1
ETTI 2008	8.1±0.8	8.9±0.8	12.9±2.6	5.6±0.7	5.0±0.8	2.2±0.2
ETTI 2009	1.1±0.1	0.4±0.3	4.0±1.1	1.6±0.5	1.3±0.3	0.6±0.4
GCKI 2008	5.0±2.0	3.3±0.0	5.8±2.5	8.3±0.7	6.7±1.0	5.0±0.5
GCKI 2009	*	1.7±0.6	*	1.7±0.6	1.7±0.6	18.3±1.4
HETH 2008	1.0±0.0	*	*	6.7±0.4	3.3±0.0	3.3±0.0
HETH 2009	1.0±0.2	2.1±0.9	3.1±0.3	5.9±0.6	*	1.7±0.3
MYWA 2008	7.7±0.2	5.9±0.8	6.5±1.8	39.2±2.8	37.2±2.2	44.8±4.4
MYWA 2009	7.5±1.8	8.6±1.6	3.2±1.3	32.0±1.6	28.5±1.9	11.7±1.4
NOCA 2008	2.1±0.7	1.7±1.0	1.7±0.3	3.5±0.2	2.1±0.2	2.4±0.5
NOCA 2009	*	*	0.4±0.1	2.1±1.3	1.0±0.2	0.7±0.1
RCKI 2008	8.8±0.5	12.6±1.0	11.3±0.8	53.3±1.5	21.7±0.5	10.0±1.0
RCKI 2009	2.1±0.7	3.1±1.0	1.7±0.4	5.0±1.0	*	2.8±0.9

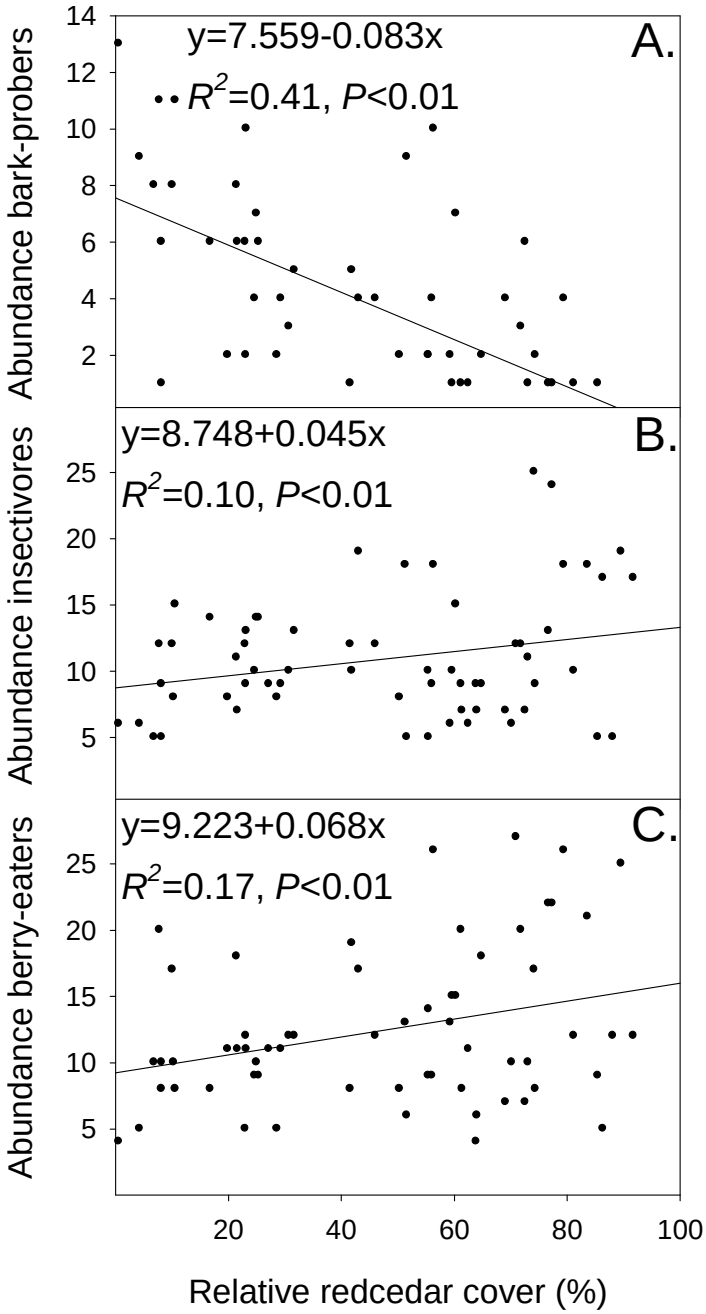

Figure 1: Significant regressions (α=0.05) of A. bark-probing birds, B. insectivorous birds, and C. berry-eating birds with relative percentage redcedar cover.

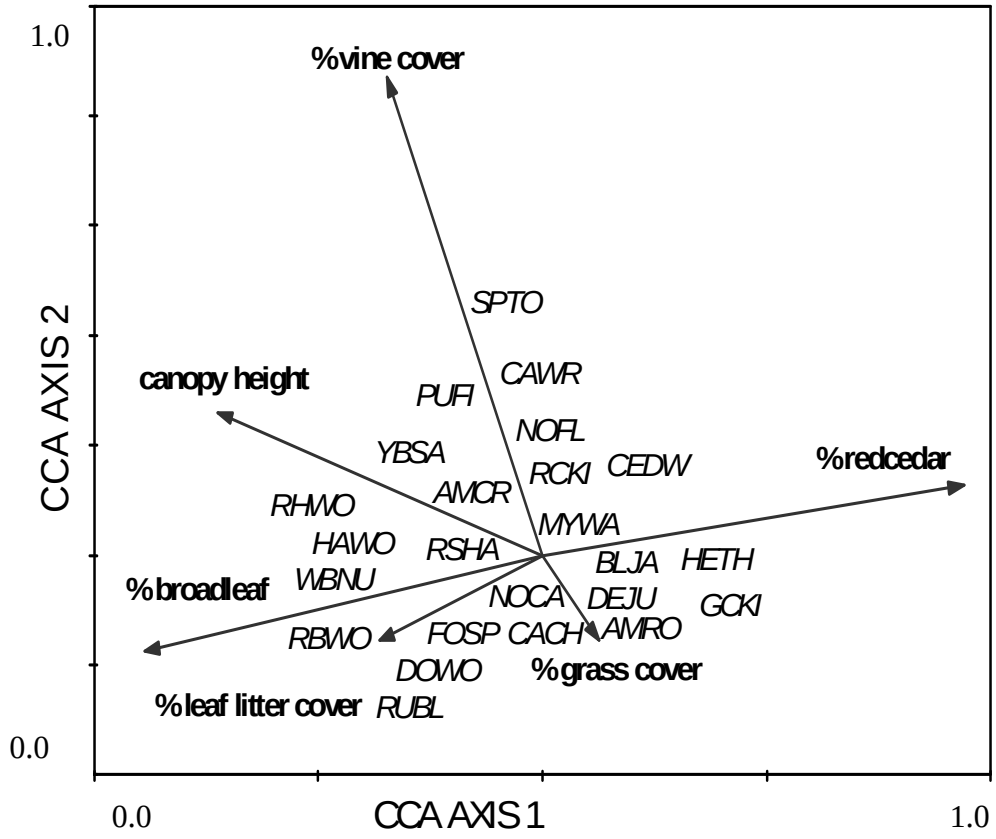

Figure 2 : CCA biplot of species and environmental variables.The first axis (λ=0.148) explains 47.8% of variation in species-environment relationship. The second axis (λ=0.058) explains 18.8%. Species codes: AMCR=American Crow, AMRO=American Robin, BLJA=Blue Jay, CACH=Carolina Chickadee, CAWR=Carolina Wren, CEDW=Cedar Waxwing, DEJU=Dark-eyed Junco, DOWO=Downy Woodpecker, ETTI=Tufted Titmouse, FOSP=Fox Sparrow, GCKI=Golden-crowned Kinglet, HAWO=Hairy Woodpecker, HETH=Hermit Thrush, MYWA=Yellow-rumped (Myrtle) Warbler, NOCA=Northern Cardinal, NOFL=Northern Flicker, PUFI=Purple Finch, RCKI=Ruby-crowned Kinglet, RBWO=Red-bellied Woodpecker, RHWO=Red-headed Woodpecker, RSHA=Red-shouldered Hawk, RUBL=Rusty Blackbird, SPTO=Spotted Towhee, WBNU=White-bellied Nuthatch, YBSA=Yellow-bellied Sapsucker.

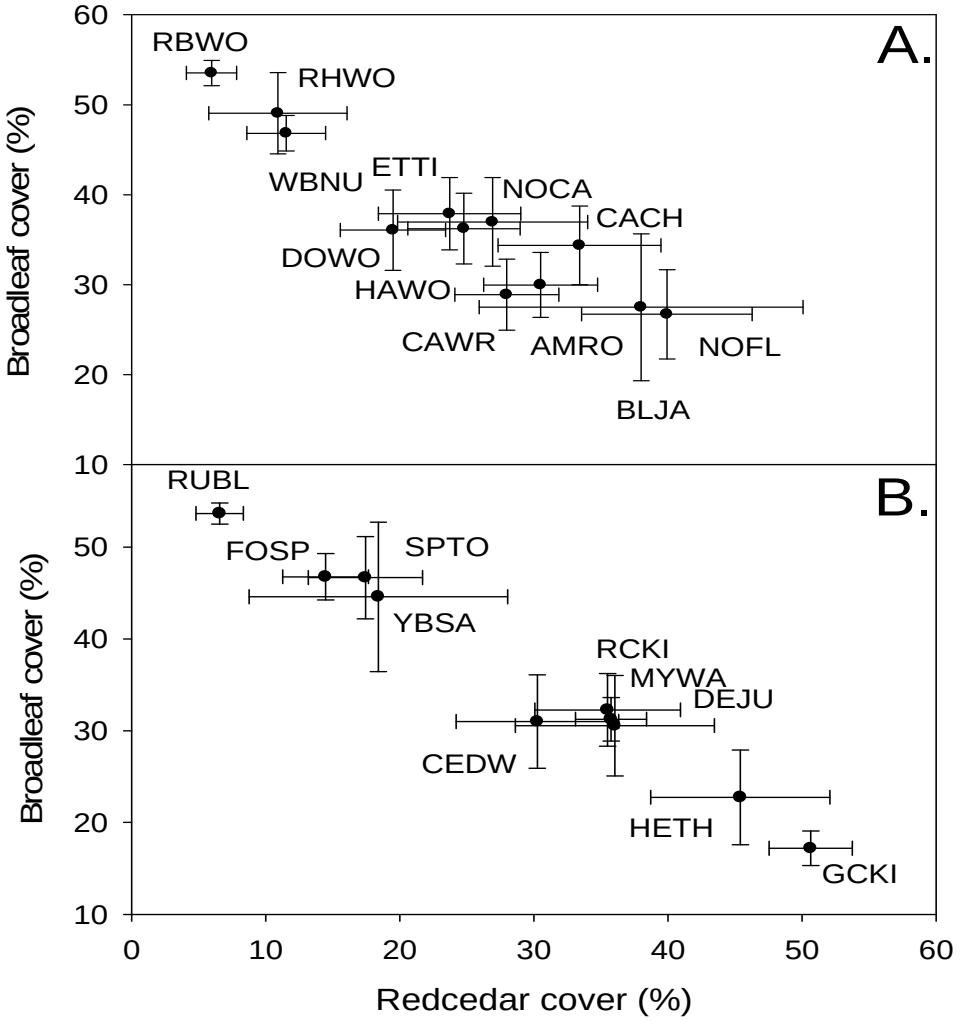

Figure 3 : Abundance centers (# individuals ≥mean for all points) of A. year-round residents and B. wintering residents in relation to cover of eastern redcedar and broadleaf species (±S.E.). Species codes: AMRO= American Robin, BLJA=Blue Jay, CACH=Carolina Chickadee, CAWR= Carolina Wren, CEDW=Cedar Waxwing, DEJU=Dark-eyed Junco, DOWO=Downy Woodpecker, ETTI=Tufted Titmouse, FOSP=Fox Sparrow, GCKI=Golden-crowned Kinglet, HAWO=Hairy Woodpecker, HETH=Hermit Thrush, MYWA=Yellow-rumped (Myrtle) Warbler, NOCA=Northern Cardinal, NOFL=Northern Flicker, RCKI=Ruby-crowned Kinglet, RBWO=Red-bellied Woodpecker, RHWO=Red-headed Woodpecker, RUBL=Rusty Blackbird, SPTO=Spotted Towhee, WBNU=White-bellied Nuthatch, YBSA=Yellow-bellied Sapsucker.

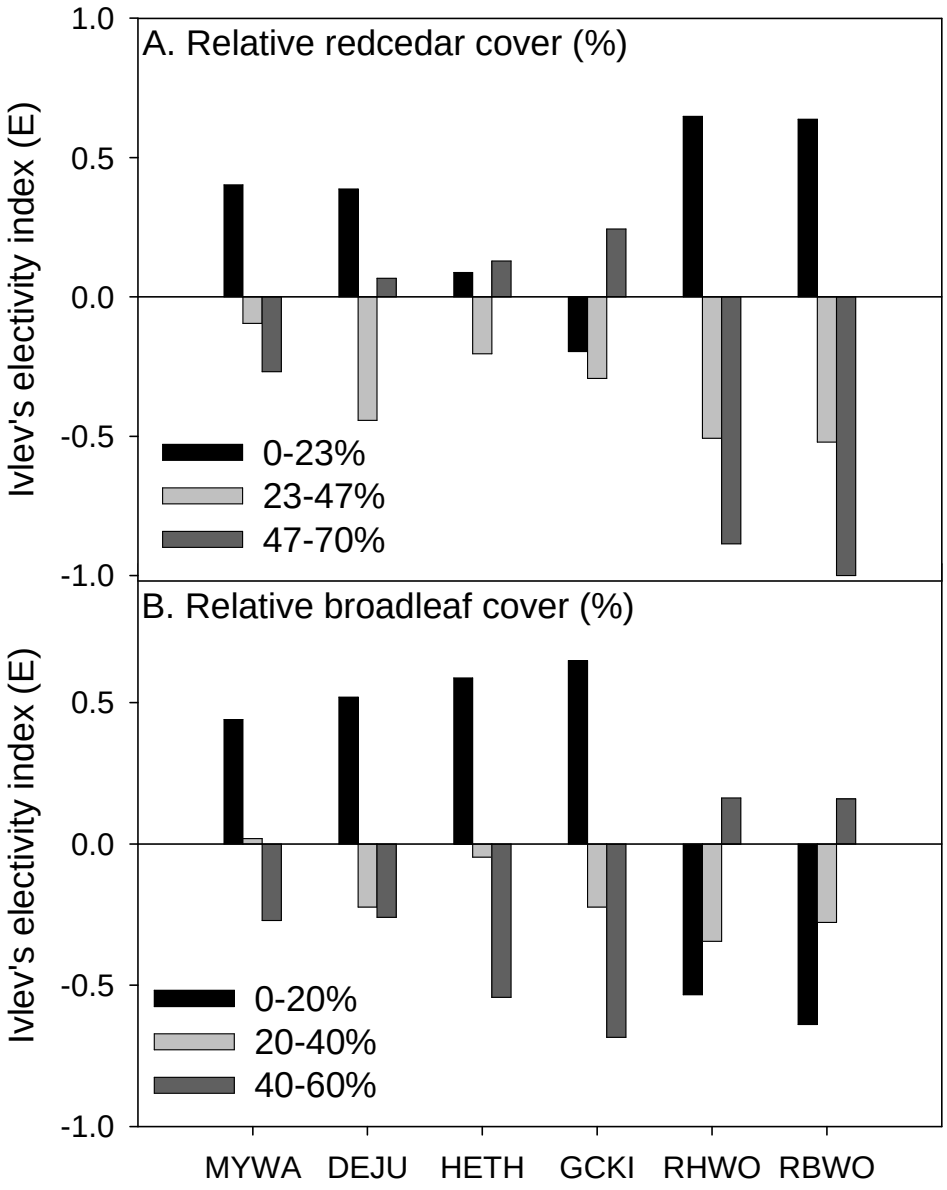

Figure 4 : Ivlev's electivity indices for select species' responses to A. three levels of redcedar cover and B. three levels of broadleaf cover. Positive values indicate that habitat was used more than expected based on availability, whereas negative values show less use.

CHAPTER V

CONCLUSION

In this thesis are two studies of similar structure, both focusing on the influence of eastern redcedar encroachment (*Juniperus virginiana* L.) in Oklahoma Cross Timber forests on biodiversity. The effects of redcedar midstory encroachment on species richness and percent cover of understory vegetation were investigated in Chapter III, while the impacts on avian species richness and composition were studied in Chapter IV.

In Chapter III, I found that both total species richness and total percentage cover of vegetation declined with increasing levels of redcedar encroachment. The main factor contributing to these decreases seemed to be the increase of redcedar leaf litter, as shown by means of simple regression and canonical correspondence analysis (CCA). A decrease in photosynthetic photon flux density (PPFD) associated with increases in redcedar canopy cover also may have contributed to changes in understory species richness and cover. Most species, including forbs and graminoids showed lower abundance in areas directly adjacent to redcedar trunks compared to other areas in the forest farther away from redcedar. Some tree seedlings and vines did not follow this pattern of frequency distribution and were most common directly under redcedar. I suggested that species that showed declines with redcedar cover did so mainly because of germination inhibition resulting from these species inability to penetrate thick litter layers due to a lack of sufficient energy stores in seeds. Shade-intolerant species such as certain forbs and grasses were less abundant under redcedar possibly due to decreases in PPFD. Species that were more abundant in the direct vicinity of redcedar likely had mechanisms to cope with thick litter layers, including larger energy stores in larger seeds. Vines had climbing or trailing mechanisms to reach areas in the forest with higher PPFD. Oak (*Quercus* spp.) seedlings were least abundant under redcedar and increased in a gradient away from

redcedar. Soil chemistry changes may be partly responsible for this decrease, as at least one species' pH tolerance levels are below the soil pH under redcedar. Changes in understory vegetation composition associated with redcedar encroachment may cause long-term alterations in forest structure as germination and growth of some overstory species such as oaks may be inhibited by increased redcedar litter loads. Declines in vegetation cover leads to diminished fine fuel loads in Cross Timbers forests, which may reduce fire frequency and promote further spread of the fire-intolerant redcedar, possibly at the expense of fire-tolerant structural dominants such as oaks.

In Chapter IV, I found that redcedar midstory encroachment altered wintering bird physiology, abundance and composition in forests. Body condition of three focal species, Yellow-rumped Warbler (*Dendroica coronata*), Dark-eyed Junco (*Junco hyemalis*) and Red-breasted Nuthatch (*Sitta canadensis*), was lower in birds captured in redcedar-dominated forest than in broadleaf-dominated forest. Avian species richness was negatively associated with increased redcedar canopy cover. Abundance of two species, Golden-crowned Kinglet (*Regulus satrapa*) and Hermit Thrush (*Catharus guttatus*) was positively related to redcedar cover, whereas woodpeckers and White-breasted Nuthatch (*Sitta carolinensis*) as a functional group of bark-probing birds showed a negative relationship. CCA revealed that an increasing gradient of redcedar canopy cover was mainly responsible for changes in avian community composition, and secondarily understory vegetation composition. Changes in forest structure associated with redcedar encroachment may be mainly responsible for changes in avian communities and physiology. Species that are linked to dense coniferous habitat during the breeding season also were most common in redcedar-encroached habitat in winter. Species related to open forests or savannas such as some woodpeckers may respond negatively to denser forest structure caused by redcedar increases because of impediments to foraging. Low body condition of birds captured in redcedar coupled with high abundance may indicate that redcedar for many species forms suitable habitat, as birds do not build up body condition to cope with unpredictable food scarcity.

The effects of redcedar on forest biodiversity are highly variable; while some taxa or groups of taxa show reduced numbers or disappear with an increase in redcedar, other taxa show no reaction or are positively affected. Changes in community composition and

abundance of one group of taxa may affect another group of taxa. Changes in forest understory vegetation associated with redcedar encroachment probably have effects on avian communities as well; reductions in vegetation cover may decrease forage and cover for birds. If redcedar promotes its own spread at the expense of broadleaf trees by reducing fine fuels, bird communities may change more drastically than described in Chapter IV. Bird and plant species (and other taxa) that respond negatively to the development of a redcedar midstory may not be able to persist once redcedar becomes the main component of forests. It would be valuable to monitor not only the effects of redcedar midstory development on taxa other than birds or understory plants. A long-term study assessing the impacts of the spread of redcedar in forests on all taxa would truly reveal the magnitude of changes in biodiversity due to fire suppression and resulting redcedar encroachment. The two studies presented in this thesis, as well as the suggested research, may be applicable anywhere woody midstory encroachment occurs in forests; a field of study that will likely gain importance as growing human populations increasingly impact forest disturbance dynamics.

APPENDICES

Appendix 1: Species found in the four forest treatments with their abundances (% cover of total sampling area per category).

Scientific name	Growth form[a]	Abundance (%)				
		Open	Oak	Out	In	Trunk
Achillea millefolium	F	0.15	0	0	0	0
Ambrosia psilostachya	F	4.18	0.38	0.85	0.15	0.23
Amorpha canescens	L	0.08	0	0	0	0
Andropogon gerardii	G	1.98	0	0.40	0	0
Antennaria parlinii	F	0	2.13	0	0	0
Asclepias syriaca	F	0.23	0.08	0	0	0
A. viridis	F	0.08	0	0	0	0
Baptisia australis	L	0.23	0	0	0	0
Boehmeria cylindrica	F	0	0.15	0.15	0.08	0
Botrychium virginianum	Fe	0	0.08	0	0	0
Bouteloua curtipendula	G	0.08	0	0	0	0
B. gracilis	G	1.03	0	0	0	0
Bromus japonicus	G	3.70	0.08	0.95	0	0
Callirhoe alcaeoides	F	0.08	0	0	0	0
Carduus nutans	F	0.15	0	0	0	0
Carex bushii	G	0.53	0.93	2.30	0.85	0.08
C. oligocarpa	G	0	0.85	0.68	0.38	0.15
C. umbellata	G	1.98	1.30	2.15	1.78	0.53
Celastrus scandens	V	0	0.40	0.08	0	0.40
Celtis laevigatus	T	0.15	0	0.30	0.63	0.30
C. occidentalis	T	0	1.73	0.98	1.35	2.20
Cercis canadensis	T	0	0.95	0.48	0.63	0.23
Chamaecrista fasciculata	L	0.48	0	0	0	0
Chasmanthium latifolium	G	0	1.95	0.15	0	0
Chenopodium album	F	0.08	0.08	0.08	0	0
Chrysopsis pilosa	F	0.78	0	0	0	0
Convolvulus arvensis	F	0	0.08	0	0	0
Cornus drummondii	T	0.08	0.78	0.23	0.23	0.15
Croton capitatus	F	0.75	0	0	0	0
C. glandulosus	F	0.75	0	0.23	0	0
Cyperus lupulinus	G	0.45	0	0.08	0.08	0

Desmanthus illinoiensis	L	0.53	0.08	0.08	0	0
Desmodium laevigatum	F	0.38	0.08	0.23	0.08	0
Dichanthelium oligosanthes	G	8.20	2.13	5.65	5.98	0.30
Diodia teres	F	0.08	0	0	0	0
Elymus canadensis	G	0.30	1.55	1.55	0.70	0.15
Eragrostis curvula	G	0	0	0.08	0	0
E. lugens	G	1.18	0	0	0	0
Erigeron strigosus	F	5.03	0.30	0.75	0.53	0.23
Eriochloa contracta	G	0.55	0.23	0.63	0.48	0
Festuca arundinacea	G	1.78	0.15	0.75	0.23	0.15
Galium aparine	F	0.08	0.40	0.08	0	0
G. circaezans	F	0.40	0.30	0.55	0.08	0.30
Gamochaeta purpurea	F	0.45	0.30	0.23	0.23	0
Geranium carolinianum	F	0.15	0.53	0.30	0.45	0.08
Geum canadense	F	0.08	2.48	1.15	0.75	0.23
Glecoma hederacea	F	0.48	0.15	0	0.08	0.08
Grindelia papposa	F	0.08	0	0	0	0
Hordeum pusillum	G	0.08	0	0	0	0
Hypericum hypericoides	F	0	0	0.08	0	0
Juncus interior	G	0.15	0	0	0	0
Juniperus virginiana	T	0.23	0.45	0.38	0.68	0.60
Lactuca serriola	F	0.15	0.48	0.08	0.08	0
Lathyrus pusillus	L	0.15	0.45	0.23	0.53	0.38
Lespedeza cuneata	F	2.60	0.88	0.48	0.15	0.08
L. procumbens	F	3.00	0	0.30	0.15	0.08
L. virginica	F	0.75	0.23	0.38	0.30	0
Liatris squarrosa	F	1.05	0.15	0.30	0	0
Melilotus officinalis	F	0.30	0	0.15	0	0
Morus rubra	T	0.40	0.08	0.15	0.08	0
Myosotis verna	F	0.08	0.38	0.08	0.15	0.70
Opuntia humifusa	C	0.08	0.15	0.08	0.08	0
O. macrorhiza	C	0	0.08	0	0	0
Oxalis acetosella	F	0.30	0	0.23	0.30	0.08
Panicum virgatum	G	0.08	0.08	0.55	0	0
Parietaria pensylvanica	F	4.95	5.88	10.08	4.70	1.23
Paronychia fastigiata	F	0.60	0	0.38	0.08	0.08
Parthenocissus quinquefolia	V	0.08	2.05	2.30	1.50	1.80
Pascopyrum smithii	G	0	1.15	0.83	0.83	1.63
Paspalum setaceum	G	0.15	0	0	0	0
Physalis longifolia	F	0.08	0	0	0	0
Phytolacca americana	F	0.08	0.48	0.95	0.08	0
Plantago major	F	0.68	0.15	0.38	0.23	0.08
Prunus angustifolia	S	1.00	0	0.15	0	0
P. mexicana	S	0.88	0	0	0	0
Quercus marilandica	T	0	0.88	0.15	0.23	0
Q. muehlenbergii	T	0	1.98	0.48	0.38	0

Q. stellata	T	0.15	1.58	1.10	1.15	0.63
Rhus glabra	S	0.30	0.70	1.18	1.00	0.23
Robinia pseudoacacia	T	0.70	0.48	0	0	0
Rubus sp.	S	0.08	0.08	0.15	0.08	0.15
Ruellia humilis	F	0.40	0	0.08	0.08	0
Sanicula canadensis	F	0.15	0.38	0.30	0.15	0.08
Sapindus drummondii	T	0	0.23	0.08	0.08	0.08
Schizachyrium scoparium	G	33.20	1.65	5.15	3.15	0
Schrankia nuttallii	L	0.15	0.15	0.08	0.08	0
Scleria pauciflora	G	0	0.15	0.08	0	0.08
Setaria gracilis	G	0.40	0	0	0	0
Sideroxylon lanuginosum	S	0.08	0.63	0.15	0.15	0.53
Smilax bona-nox	V	1.35	0.60	0.93	0.60	0.60
S. rotundifolia	V	0.08	0.75	0.15	0.85	1.28
Solidago missouriensis	F	0.08	0	0	0	0
Sonchus oleraceus	F	2.68	0	0.08	0	0
Sorghastrum nutans	G	0.08	0	0	0	0
Sorghum halepense	G	0.30	0	0	0	0
Symphoricarpos orbiculatus	S	0.08	7.60	3.55	3.63	1.08
Taraxacum officinale	F	0.30	10.63	6.48	4.18	0.53
Teucrium canadense	F	0.15	0.08	0.48	0.08	0
Toxicodendron rydbergii	S/V	0	0.08	0.55	0.15	0
Tradescantia occidentalis	F	1.58	0.55	0.55	0	0
Tragopogon pratensis	F	0.08	0.08	0.08	0	0
Triodanis perfoliata	F	0.30	0	0	0	0
Ulmus americana	T	0.15	0.23	0.78	0.93	0.38
U. rubra	T	0.15	1.83	2.40	1.90	1.13
Verbascum thapsus	F	0.08	0	0.08	0	0
Viola sororia	F	0	1.25	0.23	0.45	0.60
Vitis rotundifolia	V	0.08	0.15	0.23	0.38	0.40

Nomenclature follows USDA, NRCS, 2008. [a]Abbreviations for growth forms are: C=cactus, F=forb, Fe=fern, G=graminoid, T=tree, S=shrub, L=legume, V=vine.

Appendix 2: List of wintering bird species observed in research sites during sampling. Nomenclature follows Pyle and DeSante (2006). Species followed by asterisk were found in or directly under redcedar.

Scientific name	English name
Accipiter cooperii	Cooper's Hawk
*A. striatus**	Sharp-shinned Hawk
Aix sponsa	Wood Duck
*Baeolophus bicolor**	Tufted Titmouse
*Bombycilla cedrorum**	Cedar Waxwing
Buteo lineatus	Red-shouldered Hawk
B. jamaicensis	Red-tailed Hawk
*Cardinalis cardinalis**	Northern Cardinal
*Carduelis pinus**	Pine Siskin
C. tristis	American Goldfinch
Carpodacus mexicanus	House Finch
*C. purpureus**	Purple Finch
*Catharus guttatus**	Hermit Thrush
Certhia americana	Brown Creeper
*Colaptes auratus**	Northern Flicker
Colinus virginianus	Northern Bobwhite
Corvus brachyrhynchos	American Crow
*Cyanocitta cristata**	Blue Jay
*Dendroica coronata**	Yellow-rumped Warbler
*D. pinus**	Pine Warbler
*Euphagus carolinus**	Rusty Blackbird
*Geococcyx californianus**	Greater Roadrunner
Haliaeetus leucocephalos	Bald Eagle
*Junco hyemalis**	Dark-eyed Junco
Loxia curvirostra	Red Crossbill
*Melanerpes carolinus**	Red-bellied Woodpecker
M. erythrocephalus	Red-headed Woodpecker
*Melospiza lincolnii**	Lincoln's Sparrow
M. melodia	Song Sparrow
*Molothrus ater**	Brown-headed Cowbird
*Passerella iliaca**	Fox Sparrow
*Picoides pubescens**	Downy Woodpecker
*P. villosus**	Hairy Woodpecker
*Poecile carolinensis**	Carolina Chickadee
*Regulus calendula**	Ruby-crowned Kinglet
*R. satrapa**	Golden-crowned Kinglet
Sayornis phoebe	Eastern Phoebe
Scolopax minor	American Woodcock

*Sialia sialis**	Eastern Bluebird
*Sitta canadensis**	Red-breasted Nuthatch
S. carolinensis	White-breasted Nuthatch
*Sphyrapicus varius**	Yellow-bellied Sapsucker
*Spizella pusilla**	Field Sparrow
Strix varia	Barred Owl
*Sturnus vulgaris**	Eurasian Starling
*Thryomanes bewickii**	Bewick's Wren
*Thryothorus ludovicianus**	Carolina Wren
*Toxostoma rufum**	Brown Thrasher
Troglodytes troglodytes	Winter Wren
*Turdus migratorius**	American Robin
*Vermivora celata**	Orange-crowned Warbler
*Zenaida macroura**	Mourning Dove
Zonotrichia albicollis	White-throated Sparrow

VITA

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Candidate for the Degree of

Master of Science

Thesis: EFFECTS OF *JUNIPERUS VIRGINIANA* ENCROACHMENT ON PLANT AND AVIAN DIVERSITY IN OKLAHOMA CROSS TIMBERS FORESTS

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Scope and Method of Study: I studied changes in understory vegetation and avian communities due to eastern redcedar (*Juniperus virginiana*) encroachment into the forest midstory of oak dominated Cross Timbers west of Stillwater in central Oklahoma. I compared vegetation in forest gaps, oak dominated forest without redcedar, at the inner and outer edge of redcedar trees and near redcedar tree trunks (200 plots total). I compared avian communities and avian physiology among six circular-shaped sites, three of which had <10% redcedar cover and three of which had >80%. I also compared communities in 7x9 grid of points in a 30 ha rectangular site.

Findings and Conclusions: Species richness (11 to 6 spp. m^{-2}) and cover (53.3 to 12.7%) declined with proximity to redcedar trunks. While these declines were correlated with both increases in litter mass and decreases in photosynthetic photon flux density (PPFD), regression analysis indicated that richness (R^2=0.078) and cover (R^2=0.177) were best explained by redcedar litter mass. My study indicates that litter is the main determinant of understory vegetation declines associated with midstory encroachment in fire-suppressed forests. Decreases in herbaceous litter loads which historically contributed to the accumulation of fuel beds will have a positive feedback effect for further redcedar encroachment. Declines in oak recruitment that were related to increasing redcedar abundance and consequent increases in litter loads may lead to changes in overstory composition. Body condition was negatively correlated with redcedar canopy cover for my three focal species. Total species richness was negatively correlated with redcedar cover (r^2=0.09, P=0.02). Results indicated that food was not limiting to focal species in encroached stands, and some species occurred in higher abundance in these stands However, the effects of redcedar on birds are species dependent as bark-probing birds such as woodpeckers were negatively correlated with redcedar cover, possibly due to foraging impediments related to redcedar physical structure.

ADVISER'S APPROVAL: Rodney E. Will